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LANDSCAPE PATTERNS OF INTRAECOSYSTEM NITROGEN CYCLING

by

Donald R. Zak

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ABSTRACT

LANDSCAPE PATTERNS OF INTRAECOSYSTEM NITROGEN CYCLING

by

Donald R. Zak

Nitrogen mineralization and nitrification were studied in three upland forests differing in landscape postion, species composition and structure to gain an understanding of the spatial dynamics of intraecosystem N cycling. The ecosystems studied were an oak ecosystem associated with glaciofluvial features and two sugar maple ecosystems that occurred on morainal features but differed in ground flora composition. Stands were spatially replicated across a two county area in northwestern Lower Michigan.

Net N mineralization and nitrification potentials were determined by an eight-week aerobic laboratory incubation. Litter was collected in each ecosystem during autumn; components were separated by species and analyzed for total N. Litter production, N returned to the forest floor, N mineralization and nitrification in both sugar maple ecosystems were two times greater than in the oak ecosystem. Nitrification potentials were minimal in the oak forest. Nitrification was four times greater in the species-rich sugar maple ecosystem compared to the species-poor sugar maple ecosystem. High nitrification potentials were

consistently related to the distribution of spring ephemeral communities.

Seasonal fluxes of N mineralization and nitrification were estimated using a buried polyethylene bag technique; surface soil samples were incubated at monthly intervals for one year. Aboveground woody biomass and its allocation to annual increment were determined using species-specific allometric biomass equations. Distinct patterns of overstory production, mineralization and nitrification corresponded to the spatial distribution of forest ecosystems. Nitrogen mineralization was 86.1 kg ha^{-1} yr^{-1} in the oak ecosystem; significantly less than annual mineralization in the sugar maple forests (106 kg ha^{-1} yr^{-1}). Nitrification was greatest in the species-rich sugar maple forest; 82% of all mineral N was oxidized to NO_3^- (88.1 kg ha^{-1} yr^{-1}). Nitrification in the oak forest was 5% of mineral N production (4.5 kg ha^{-1} yr^{-1}). The spatial distribution of forest ecosystems could be used to predict landscape patterns of N mineralization and nitrification.

Nitrate reductase (NR) activity was measured in Allium tricoccum and Asarum canadense to investigate the mechanism of N retention by spring ephemeral communities. NR activity was low in both species, indirectly suggesting NH_4^+ assimilation and plant-nitrifier competition as a possible mechanism of N retention.

This work is dedicated to my parents and wife
who are a constant source of love
and encouragement in my life.

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I express deep appreciation to Dr. Kurt S. Pregitzer for his guidance, inspiration and friendship throughout my graduate studies. Few people in my life have so willingly shared of themselves to help me develop personally and professionally. The skills and attitudes I have acquired from him will undoubtedly be of great value throughout my life.

A sincere thanks is extended to Drs. James Hanover, James Hart, Peter Murphy and James Tiedje who served as members of my graduate committee. Their advice and encouragement were invaluable through this research. I am indebted to Dr. Phu Nguyen for countless hours of advice and assistance with the analytical portions of this study. Dr. Peter Groffman reviewed many of the chapters in this dissertation; I sincerely thank him.

I have gained a great deal from my colleagues in the Forest Ecology Lab and in return, I hope I have contributed something to them. In particular, I would like to acknowledge George Host. Over the last 3 and one half years, we have worked closly together; I have the highest regard for him personally and professionally. Bill Cole, Peter Greaney, Jim Cotner and Donna Zak assisted with sample collection, even on cold rainy days in November.

Most importantly, I would like to thank my wife, Donna, for all her love, understanding and encouragement, and my son Joseph who is a constant reminder of the truly important things in life.

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Chapter I

INTRODUCTION

While nitrogen is thought to be a key nutrient limiting the growth of many temperate forests, little is known regarding the spatial dynamics of intraecosystem N cycling across regional and local landscapes. Lohnis (1913) was perhaps the first to conceptualize the N cycle and since, numerous advances have been made toward understanding the processes regulating the flow of N within terrestrial ecosystems. Studies concerned with defining patterns and processes of intraecosystem N cycling have been conducted in many different forest types, and significant global patterns have emerged (Cole and Rapp 1982; Flanagan and Van Cleve 1983; Grub 1977; Gosz 1981; Melillo 1981; Weber and Van Cleve 1981). However, most studies have been point-specific and spatial patterns of intraecosystem N cycling, similar to landscape patterns of forest composition and structure, have received little attention.

The ability to extrapolate point-specific N cycling information across regional and local landscapes is of fundamental importance for prudent land management. For example, forest management typically alters intraecosystem N cycling at the scale of 10 to 100 hectares. Silvicultural practices, such as clear cutting and herbicide application,

eliminate plant uptake and favor conditions for N loss. Vitousek and Melillo, (1979) in a literature review of NO_3^- loss following timber harvest found losses to vary widely among forest types. Vitousek et. al. (1982) suggested that N losses could be subdivided into three components i) the predisturbance N mineralization rate and the extent to which it is elevated following canopy removal, ii) an interaction of processes which delay or prevent loss of excess mineralized N and iii) the rate at which vegetation re-establishes. More simply stated, regulation of NO_3^- loss occurs through an interaction involving plant uptake, mineralization, immobilization and nitrification. We know a great deal regarding the physiology and microbiology of the processes regulating N availability and loss in forest ecosystems. We lack, however, the conceptual and empirical foundation that facilitates the spatial extension of this knowledge across large land areas.

In addition to its relevance to forest management, spatially oriented studies of dynamic ecosystem properties may provide further insight into the basic organization of forest ecosystems. Watt (1947) was perhaps the first advocate of such an approach and suggested that broader understanding of community dynamics could be gained if studied from a temporal and spatial perspective. McNaughton (1983), in a study of the Serengeti grasslands, proposed that climate, geology and topography impose the primary constraints which direct ecosystem development, soil formation and the evolution of grazing web members. In Michigan, the distribution of forest communities is integrally related to landscape patterns of physiography and soil (Pregitzer and Barnes 1982, 1984). Do environmental factors which influence landscape patterns of forest composition and structure further regulate spatial patterns of dynamic ecosystem processes? The primary aim of my research was to gain an understanding of the spatial pattern of intraecosystem N cycling within a forested landscape by integrating environmentally and biologically important factors that influence not only N turnover, but also ecosystem development.

An Approach for Defining Spatial Patterns of Intraecosystem N Cycling

Forest ecosystems are readily identifiable within the landscape, and lend themselves to mapping at various scales (Bailey 1985). In Michigan, ecosystem classification studies have demonstrated that spatial variation in forest composition and structure can be explained using combinations of landform, soil and vegetation (Pregitzer and Barnes 1982, 1984). An understanding of the spatial variation of intraecosystem N cycling may be gained by conducting nutrient cycling studies within the framework of an ecosystem classification system. This method has effectively explained the landscape distribution of forest communities.

During the 1983 field season, I participated in the development of an Ecological Classification System for the Manistee National Forest. Vegetation, soil and forest productivity data were collected in 58 stands representative of the upland forest communities of Manistee and Wexford Counties, Michigan. Stands were classified into ecosystems using an integrated multifactor system (Barnes et al. 1982; Pregitzer and Barnes 1984). I selected three upland forest ecosystems that differed in landscape position, species composition and structure to study the spatial variation of N turnover. They were an oak ecosystem associated with glaciofluvial landforms and two sugar maple ecosystems that occurred on morainal features but differed in ground flora composition. These types of forests repeatedly occur across much of northern Lower Michigan.

The research presented here represents a chronological series of investigations; the results of one study fostering the initiation of the next. In Chapter II, I hypothesized that spatial patterns of N mineralization and nitrification were related to the landscape distribution of forest ecosystems. This was tested by comparing laboratory N mineralization and nitrification potentials among the upland forests. *In situ* seasonal fluxes of N mineralization and nitrification were determined in Chapter III and compared with overstory and litter production. From these studies, a significant pattern emerged between NO_3^- availability and the distribution of ground flora communities. Specifically, the distribution of diverse spring ephemeral and herbaceous ground flora communities was consistently related to high nitrification potentials. Muller and Borman (1978) suggested that these communities represent a "vernal dam" retaining nutrients within forest ecosystems at a time when they are likely lost. In addition, Blank et al. (1980) found uptake by spring ephemeral communities to be sufficient to affect ecosystem level fluxes of N. The mechanism of N retention by these communities was investigated in Chapter IV.

A Description of Three Upland Forest Ecosystems

The sugar maple-basswood/*Osmorhiza* ecosystem occurred on the finer-textured morainal landforms of Wexford County. Topography within the Interlobate moraine is complex with numerous small drainages that vary in slope and aspect. In general, the sugar maple-basswood/*Osmorhiza* forests are restricted to the northerly aspects; slope position is variable. Slopes typically range from 0 to 40%. Soils belong to the Kalkaska series (sandy, mixed, frigid, Typic Haplorthod) and have formed in fine sands to loam parent materials; silt + clay fractions were approximately 3% of the total particle weight. The typical horizon sequence is O-A-E-Bhs-Bs-C.

The sugar maple-basswood/Osmorhiza ecosystem was typified by high species richness and well-developed stand structure. The overstory was dominated by Acer saccharum and Tilia americana, averaging 10.1 and 8.0 m^2/ha basal area, respectively. Fagus grandifolia, Prunus serotina and Fraxinus americana were also common overstory associates. Quercus rubra was uncommon, averaging 2.1 m^2/ha of basal area. The association has a well developed understory, which was absent in the other northern hardwoods forest. Representative understory species include Ostrya virginana and numerous Acer saccharum saplings. The ground flora was characterized by a diverse assemblage of herbaceous perennials and ephemerals. Percent coverage of the forest floor was typically greater than 80%. Characteristic species included Osmorhiza chilensis, Mitella diphylla, Viola canadense, and Uvularia perfoliata. The spring ephemeral community was particularly well developed, with Allium tricoccum, Dicentra canadense, D. cucullaria, Erythronium americana and Claytonia caroliniana dominant species.

The sugar maple-red oak/Maianthemum ecosystem occurred on the Interlobate moraine in the northern portion of Wexford County. This ecosystem is found in landscape positions similar to the sugar maple-basswood/Osmorhiza ecosystem, but typically on slightly coarser soils and usually on southerly exposures. Soils typically form in medium to fine sands, and also belong to the Kalkaska series. The typical horizon sequence is O-A-E-Bs-C.

The overstory of the sugar maple-red oak/*Maianthemum* ecosystem was dominated by *Acer saccharum* and *Quercus rubra*, averaging 10.3 and 10.1 m^2/ha of basal area, respectively. *Prunus serotina*, *Tillia americana* and *Fraxinus americana* were uncommon. Species richness was lower and stand structure was simpler than that of the sugar maple-basswood/*Osmorhiza* ecosystem. The understory layer was not well developed and had an open appearance. The ground flora was relatively depauperate and coverage of the forest floor was sparse, typically less than 10%. The spring ephemeral community was represented by two species: *Erythronium americanum* and *Claytonia caroliniana*. *Maianthemum canadense*, *Trientalis borealis* and *Lycopodium lucidulum* were present throughout the growing season. *Acer saccharum* seedlings were very abundant, but saplings were uncommon.

The black oak-white oak/*Vaccinium* ecosystem occurred on moraines, ice contact hills and outwash plains. Physiography is variable, ranging from level on the outwash plains to 30% slopes on the morainal features. However, the ecosystem was typically found on outwash plains. Soils are well drained sands; medium and fine sand account for 94% of the total particle weight. The soil series is a Rubicon; a sandy, mixed, frigid, Entic Haplorthod. The typical horizon sequence is O-A-E-Bs-C.

The black oak-white oak/Vaccinium ecosystem differed dramatically from the northern hardwood forests in composition and structure. Stand stocking was low, allowing ample light to reach the forest floor. This condition was different from the sugar maple forests, where the canopy was closed, allowing little light to pass through. The overstory was composed primarily of two species: Quercus velutina and Q. alba. This association lacks an understory, but the low shrub layer was well-developed and dominated by Vaccinium angustifolium and Gaylussacia baccata. The spring ephemeral community was totally absent in this ecosystem, but there was an abundant ground flora dominated by woody ericaceous species, particularly Gaultheria procumbens and Michella repens. Common herbaceous species included: Carex pensylvanica and Comandra umbellata. Leucobryum glaucum and Dicranum polysetum were common.

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Chapter II

LANDSCAPE VARIATION IN NITROGEN MINERALIZATION AND NITRIFICATION

Abstract

Potential nitrogen mineralization and nitrification were studied in three upland forest ecosystems to develop an understanding of nitrogen turnover on a landscape basis. The northern Michigan forests studied were an oak ecosystem primarily associated with glacial outwash features, and two sugar maple ecosystems which occur on morainal landforms but differed in the diversity and abundance of ground flora species. Four randomly chosen stands separated by at least 6 km were sampled within each of the three ecosystems. Potential net nitrogen mineralization and nitrification were determined by an aerobic laboratory incubation. Litter was collected from all ecosystems during autumn. Litter production, nitrogen returned to the forest floor, and net mineralization differed by a factor of two between the oak and sugar maple ecosystems. Nitrification was four times greater in the species-rich sugar maple ecosystem compared to the species-poor sugar maple ecosystem. Nitrification was virtually absent in the oak ecosystem. The spatial distribution of ecosystems could be used to predict differences in potential mineralization and nitrification.

Areas susceptible to nitrate loss following intensive forest management practices may be related to the occurrence of plant associations. In this upland landscape, high nitrification potentials appear to be confined to species-rich sugar maple forests.

Introduction

Nitrogen cycling within forest ecosystems is regulated by a complex interrelationship among plant uptake, the quality and quantity of plant litter returned to the soil, and mineralization of organic N through the activities of soil microorganisms. The rate at which N is made available for plant growth is dependent on the process of mineralization. In turn, the rate at which plant material is mineralized is related to the amount of litter returned to the forest floor and its chemical composition. Soil moisture directly affects N mineralization by regulating the activities of soil microorganisms and influencing the production of recalcitrant plant litter (Aber and Melillo 1982; Melillo et al. 1982; Vitousek 1982).

Studies concerned with defining patterns and processes of intraecosystem N cycling have been conducted in numerous forest ecosystems and strong global patterns of N cycling have emerged (Flanagan and Van Cleve 1983; Grubb 1977; Gosz 1981; Melillo 1981; Weber and Van Cleve 1981; Cole and Rapp 1982; Vitousek 1982). It is not surprising that the distribution and cycling of N within boreal, temperate, and tropical ecosystems is quite different. However, we know very little about the variability and predictability of intraecosystem N cycling across regional and local landscapes.

Comparative N cycling studies such as those conducted by Vitousek et al. (1982) have shown a high degree of variation among temperate forests from similar geographic regions. For example, differences in potential mineralization and nitrification between an oak-maple and northern hardwood site in New England were as large as between a Ponderosa pine site in New Mexico and an oak site in Indiana (Vitousek et al. 1982). In addition to regional climate, much of this variability is undoubtedly due to differences in the dominant vegetation, since litter quality exerts a strong influence on mineralization and nitrification (Aber and Melillo 1982; Melillo et al. 1982; Vitousek 1982).

Pregitzer and Barnes (1984) have shown that patterned variation in forest composition and structure is effectively explained using combinations of landform, soil, and vegetation. Pastor et al. (1984) have demonstrated that species replacement along a moisture gradient exerts a significant influence on N cycling. Since litter quality is related to community composition, landscape patterns of species composition should strongly influence the process of N mineralization. We have hypothesized that variation in N mineralization and nitrification is strongly related to the spatial distribution of forest ecosystems.

We tested our hypothesis by comparing potential N mineralization and nitrification among three ecosystems widely distributed across northern Lower Michigan. Stands within each ecosystem were replicated spatially in an attempt to develop an understanding of landscape variability in N mineralization and nitrification.

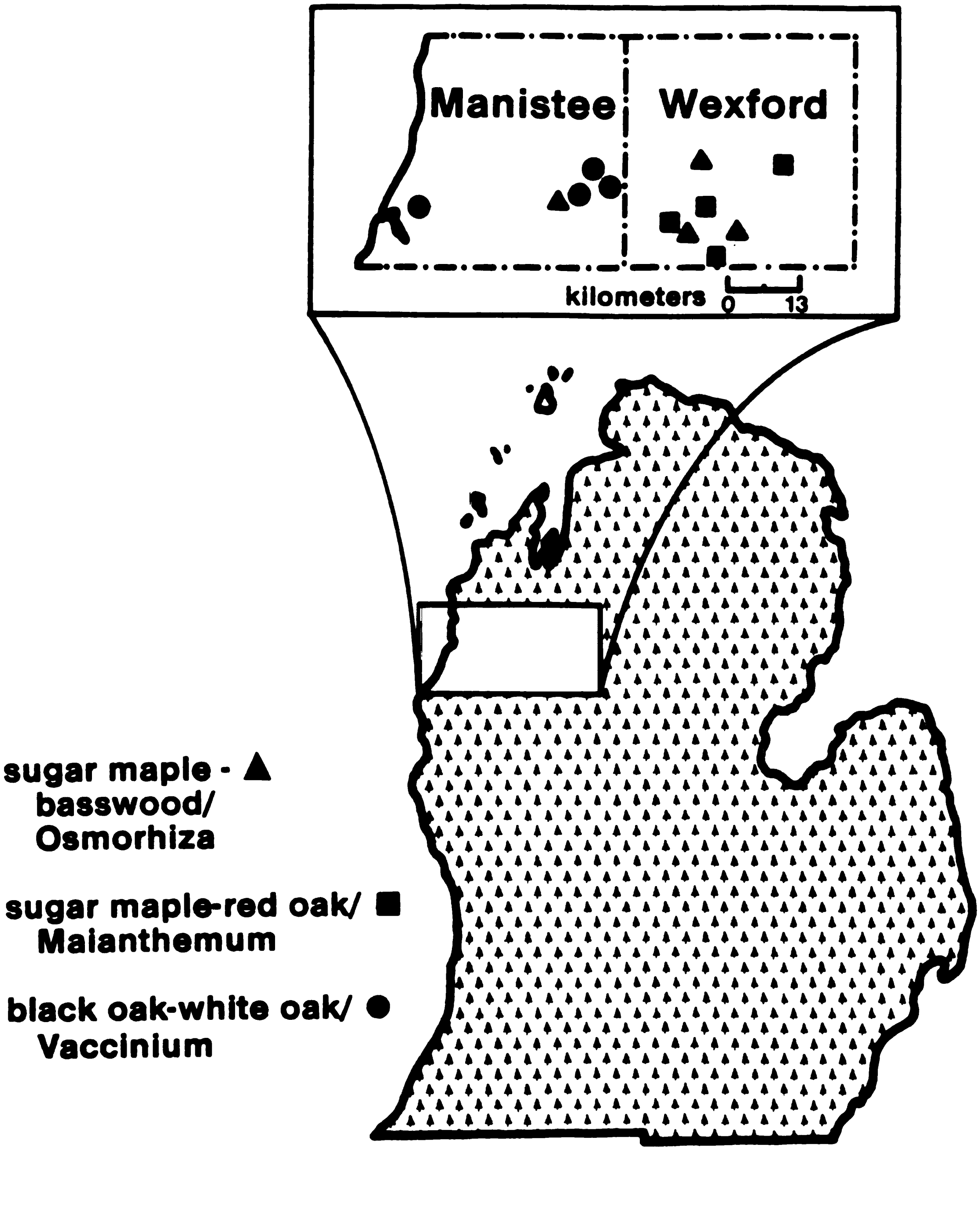
Methods

Study Area

The study occurred in upland forests of Manistee and Wexford Counties, northwestern Lower Michigan (Figure 2.1). Lake Michigan lies directly to the west and exerts a major climatic influence in the western portion of the study area. Mean annual precipitation of 81 cm is evenly distributed throughout the year. Mean annual temperature is 7.2^{o}C and the length of the growing season varies from 150 days near Lake Michigan to 100 days 60 km inland.

The Interlobate moraine which transects the northern portion of Wexford County is a predominant feature in the landscape (Farrand and Eschmann 1974). The maximum elevation of the morainal system is 335 meters above sea level. Soils on this landform were primarily Typic Haplorthods. The Port Huron moraine extends into northern Manistee county; Entic Haplorthods are the most common soils. A network of outwash plains dominates the landscape in the southern portion of Manistee County. Typic Udipsamments have developed in the most xeric portions of these outwash plains, while Entic

Figure 2.1 Distribution of stands within three upland forest ecosystems in Manistee and Wexford Counties, Michigan U.S.A.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Wexford
kilometers 0 13
sugar maple - ▲ basswood/ Osmorhiza
sugar maple-red oak/ ■ Maianthemum
black oak-white oak/ ● Vaccinium

Haplorthods were found where conditions were slightly more mesic.

During the 1983 field season, vegetation, soil and forest productivity data were collected from 58 stands within the study area. Stands were 1 ha or larger and exhibited no evidence of recent disturbance. Stands were classified into ecosystems based on combinations of landform, soil and vegetation (Barnes et al. 1982; Pregitzer and Barnes 1984). Three upland ecosystems were chosen for this study: an oak ecosystem and two sugar maple ecosystems which differed in ground flora composition. Four stands in each of the three ecosystems were randomly selected in 1984 from the pool of 58 stands previously sampled. The stratified random sampling scheme provided replication across a two county area (Figure 2.1).

The three ecosystems studied were: sugar maple-basswood/Osmorhiza, sugar maple-red oak/Maianthemum and black oak-white oak/Vaccinium. The names used are convenient abbreviations for the classification units. Sugar maple-basswood/Osmorhiza, for example, represents the current dominant overstory and characteristic ecological species group, but the names used here connote more than plant communities. They represent integrated landform, soil and vegetation classfication units (Barnes et al. 1982).

The ecosystems represent a series of relatively late successional upland communities that repeatedly occur across thousands of hectares in northern Lower Michigan. They also represent a moisture-edaphic gradient with sugar maple-basswood/Osmorhiza occupying the most mesic conditions. The sugar maple ecosystems consistently occurred on the Interlobate moraine while the black oak-white oak/Vaccinium ecosystem consistently occurred on the xeric portions of the Port Huron moraine and outwash plains.

Vegetation and Soil Analysis

In each stand, four 5 m x 30 m plots were randomly located for vegetation and soil sampling. Within the plots, percent cover and frequency were determined for herbaceous and woody vegetation less than 2.5 cm dbh. Percent cover was determined by ocular estimation for each species by a modification of Braun-Blanquet's cover abundance scale (Braun-Blanquet 1932). Percent frequency was determined using six 1-m^2 frequency frames systematically located along the long axis of each plot. Understory vegetation was sampled using stem counts. The overstory was sampled using a 10 BAF (English) point sample at the center of each plot, and total and merchantable heights were measured for each tally tree.

Soil samples were collected from 24 points within a stand: six samples in each of the four randomly located plots. Samples were taken from within the 1-m^2 frequency frames used in sampling the ground-flora. Soil samples consisted of a core 100 cm^2 and 2.5 cm in depth excavated from just below the loose litter. Thus, samples were taken from the top of the A horizon in the sugar maple ecosystems and the Oe horizon in the oak ecosystem. Shallow soil samples were used to avoid "priming effects" created by the mixing of organically-enriched surface horizons with deeper mineral horizons (Salonius 1978). Mixing of horizons may lead to an over-estimation of potential N mineralization and nitrification (Thorne and Hamburg 1985). The samples were placed undisturbed into polyethlyene bags, refrigerated and returned to the laboratory for analysis. Subsurface soil samples were collected from one location in each plot and composited on a stand basis. Soil pH was determined from a 1:1 soil-deionized water paste (McLean 1982). The Walkley-Black method was used to determine soil organic carbon (Walkley 1947). Silt + clay content in B horizon samples was determined by wet sieving.

Potential N mineralization and nitrification were determined by aerobic soil incubation (Vitousek et al. 1982). Soil samples were sieved and material greater than 2 mm was excluded. Two 10 g subsamples were taken from the sieved material for the incubation assay. One 10 g subsample was extracted with 2 N KCl and analyzed for NH_4^+-N and NO_3^--N using a Technicon Autoanalyzer II. NH_4^+-N was determined by color development with Na-phenolate (Technicon 1976). Reduction with Cd followed by color development with sulfanilamide and napthylethylenediamine was used to determine NO_3^--N (Technicon 1976).

The second 10 g subsample was incubated at 30° C and 80% relative humidity in the dark for 8 weeks. During the incubation, the soil samples were maintained at 0.03 MPa moisture tension by the addition of deionized water. Percent moisture at 0.03 MPa was determined previously with a pressure plate on randomly selected subsamples from each plot. Following incubation, samples were analyzed for NH_4^+-N and NO_3^--N by the above-mentioned procedure. Potential N mineralization was determined as the increase in NH_4^+-N plus NO_3^--N in incubated samples over initial amounts. Similarly, potential nitrification was determined as the amount of NO_3^--N accumulated in incubated samples over initial amounts.

Litter Analysis

Plant litter was collected during September and October 1984. One stand was randomly selected for sampling in each of the three ecosystems. Ten litter traps were randomly placed among the four plots in each stand. The contents of each 250-cm^2 trap were collected at 3-week intervals and returned to the laboratory where litter was oven-dried at 80° C for 24 hrs. Material from each trap was sorted by species and separated into leaf and seed fractions. The sorted litter was redried and weighed to determine the weight of litterfall on an areal basis. Each sample was then ground in a Wiley mill and digested with concentrated H_2SO_4 and K_2SO_4 - HgO as a catalyst in a block digestor. The digestate was analyzed for total N using a Technicon Autoanalyzer II (Technicon 1977). N concentrations and litter weight were used to calculate the amount of total N returned to the forest floor during autumn litter fall.

Statistical Analysis

Mineralization data were analyzed using analysis of variance (ANOVA) for a completely randomized design with replication. A one way ANOVA and a nested (ecosystem x stand) ANOVA were performed on mineralization and nitrification data (SAS 1982). Mean mineralization, nitrification and litter N content at the stand level were compared using a protected Fisher's LSD procedure. Paired t-tests with a pooled estimation of variance were used to compare litter weight (kg/ha), N concentration (%), and N content (kg/ha) for species common to two ecosystems. T-tests were used since individual overstory species were often found in two, but not in all three ecosystems.

Ground-flora data were analyzed using principal component analysis (SAS 1982). All herbaceous species and woody species less than 1.3 cm dbh present in 10% or more of the plots were included in the analysis. Because ground flora composition was relatively heterogeneous, presence/absence (binary) data were used (Strahler 1977).

Results

Vegetation

Stand ages were not significantly different; mean age for the oak ecosystem was 68 years and mean age for both sugar maple ecosystems was 63 years (Table 2.1). Basal area was highest in the sugar maple-basswood/*Osmorhiza* ecosystem (28.3 m^2 ha^{-1}) and lowest in the black oak-white oak/*Vaccinium* ecosystem (23.5 m^2 ha^{-1}). The same pattern was present in gross merchantable volume, with the sugar maple-basswood/*Osmorhiza* system carrying the greatest volume (Table 2.1).

The ecosystems were quite distinct in ground flora composition. The locations of plots along the first two principal component axes show that ecosystems are clearly separated according to differences in ground flora (Figure 2.2). Moreover, the relatively tight groupings of plots within ecosystems indicates that there is a consistent pattern of ground flora vegetation associated with the characteristic physiography, soil, and overstory of these ecosystems.

Table 2.1 Overstory and soil summary of three forest ecosystems in northern Lower Michigan. Numbers represent mean values (standard error of the mean) for individual ecosystems.

	black oak-white oak/ *Vaccinium*	sugar maple-red oak/ *Maianthemum*	sugar maple-basswood/ *Osmorhiza*
	Ecosystem means		
I. Overstory			
Trees/ha	943 (141)	742 (121)	881 (209)
Basal area (m^2/ha)	23.5 (0.1)	25.0 (2.6)	28.3 (3.8)
Volume[1] (m^3/ha)	166.7 (12.7)	207.2 (30.2)	261.2 (26.4)
Stand age (yrs)	68 (2.7)	63 (0.9)	63 (2.1)
II. Soil			
0 to 2.5 cm			
Organic C (%)	2.64 (0.19)	2.61 (0.28)	4.51 (0.58)
pH	3.98 (0.02)	4.29 (0.06)	5.66 (0.05)
B Horizon			
silt + clay (%)	4.1 (1.3)	5.0 (1.5)	10.2 (2.1)

[1] gross merchantable volume to a 10.2 cm top.

Figure 2.2 Principal component analysis (PCA) of 48 plots from three upland forest ecosystems. PCA was based on ground flora presence/absence data. Numbers represent ecosystem designations: 1 black oak-white oak/*Vaccinium*, 2 sugar maple-red oak/*Maianthemum*, and 3 sugar maple-basswood/*Osmorhiza*

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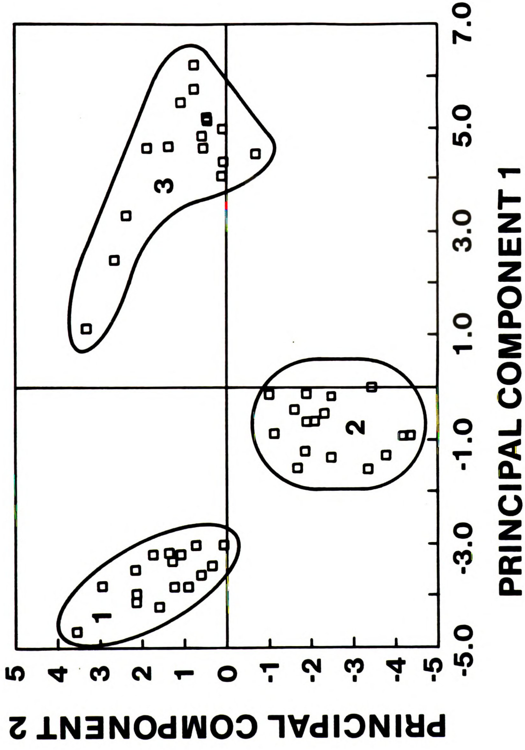

Potential N Mineralization and Nitrification

Soil pH and organic carbon increased across the ecosystem gradient. The black oak-white oak/Vaccinium ecosystem had the lowest pH and organic carbon levels (Table 2.1). Soil pH was higher in the sugar maple-red oak/Maianthemum ecosystem, but organic carbon was not different. The sugar maple-basswood/Osmorhiza ecosystem exhibited the highest pH and organic carbon content (Table 2.1). The amount of silt + clay in the B horizon also differed among the ecosystems and increased from 4.1% in the black oak-white oak/Vaccinium ecosystem to 10.2% in the sugar maple-basswood/Osmorhiza ecosystem (Table 2.1).

The amount of N mineralized during the 8 week incubation differed significantly among the three ecosystems, paralleling soil pH. The black oak-white oak/Vaccinium ecosystem exhibited the lowest potential mineralization (111 ug N/g). Potential mineralization increased to 196 ug N/g in the sugar maple-red oak/Maianthemum ecosystem and was greatest in the sugar maple-basswood/Osmorhiza ecosystem, with 263 ug N/g produced during the incubation (Figure 2.3).

Variability was directly proportional to mineralization. Stand-to-stand variability was low in the black oak-white oak/Vaccinium ecosystem, was higher in the sugar maple-red oak/Maianthemum ecosystem and reached a maximum in the sugar maple-basswood/Osmorhiza ecosystem (Figure 2.3). With the

Figure 2.3 Potential N mineralization of three upland forest ecosystems. Values represent stand means for the amount of ammonium + nitrate produced during an eight week aerobic laboratory incubation. Ecosystem means are represented by the broken lines. Ecosystem means with the same letter are not significantly different (alpha = 0.05).

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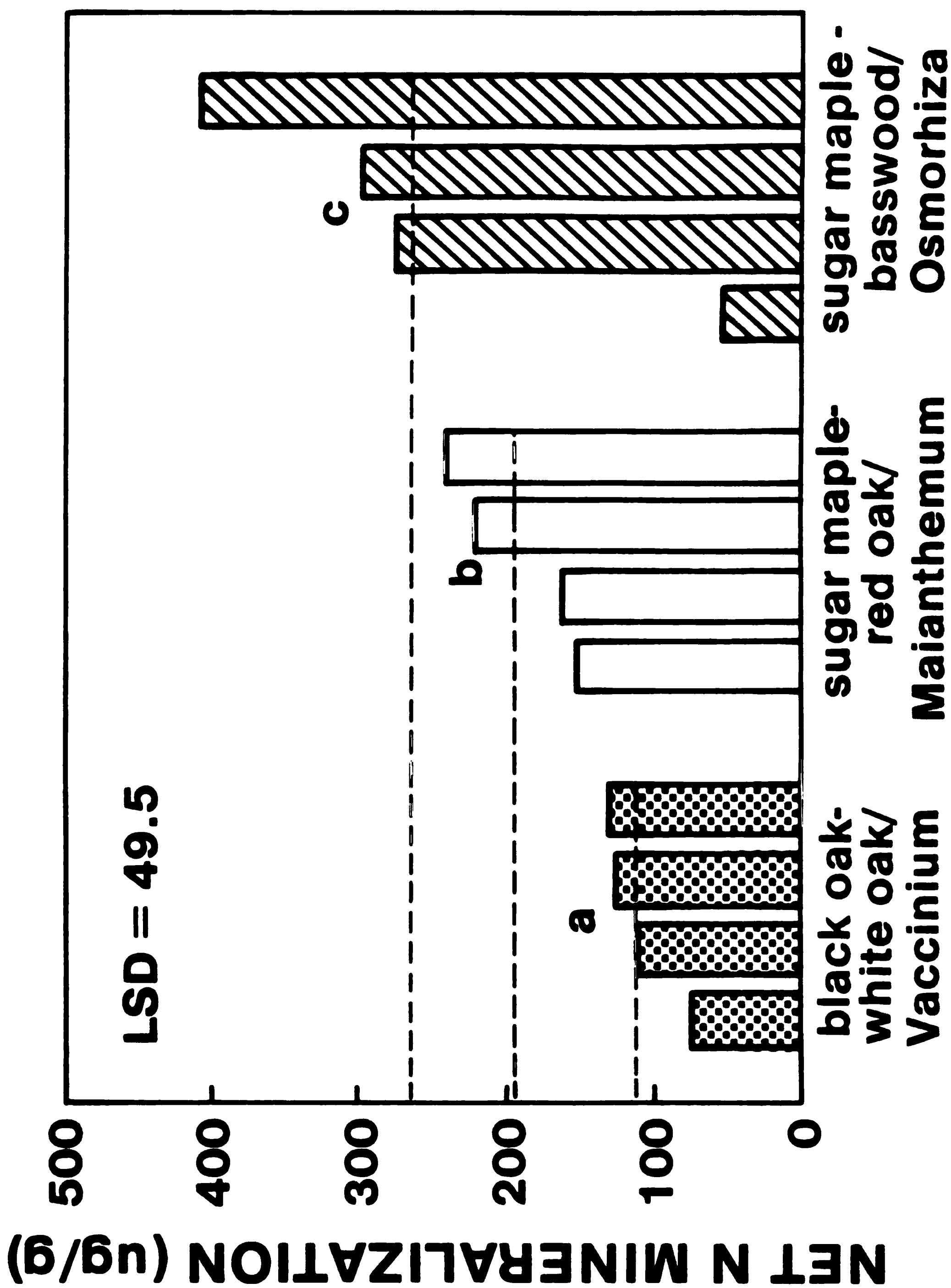

exception of one stand, there was no overlap among the ecosystems (Figure 2.3). These results are in agreement with Powers (1980), who found variability increased along with average amounts of potential mineralization.

The pattern of potential nitrification was similar to potential mineralization; ecosystem means were significantly different. A proportional relationship existed between mineralization and nitrification. Potential nitrification was very low in the black oak-white oak/*Vaccinium* ecosystem, with an average of only 2 ug NO_3^--N/g produced during the 8 week incubation. Potential nitrification was 48 ug NO_3^--N/g and 158 ug NO_3^--N/g in the sugar maple-red oak/*Maianthemum* and the sugar maple-basswood/*Osmorhiza* ecosystems, respectively.

Litter

Mean litterfall (kg/ha) was not significantly different between the two sugar maple stands (Table 2.2). However, litterfall was significantly lower in the black oak-white oak/*Vaccinium* stand, about one-half that of the sugar maple forests. Sugar maple accounted for 44% of the total litterfall in the sugar maple-basswood/*Osmorhiza* stand. Basswood (*Tilia americana* L.) and white ash (*Fraxinus americana* L.) contributed a large proportion of the total litterfall, 23% and 18%, respectively. In contrast, sugar

Table 2.2 Weight and total N content of leaf and seed litter by ecosystem and species. Numbers represent average values for one stand within each ecosystem.

Species	ECOSYSTEM: black oak-white oak / *Vaccinium*			sugar maple-red oak / *Maianthemum*			sugar maple-basswood / *Osmorhiza*		
	Litter Weight (kg/ha)	N Conc. (%)	N Content (kg/ha)	Litter Weight (kg/ha)	N Conc. (%)	N Content (kg/ha)	Litter Weight (kg/ha)	N Conc. (%)	N Content (kg/ha)
1. Leaves									
Acer saccharum				642	0.74*	4.63	1150	1.02*	10.16
Tilia americana				4	0.82*	0.03	586	1.57*	9.09
Fraxinus americana							470	1.02	5.03
Ostrya virginiana				10	1.35	0.13	76	1.38	1.21
Fagus grandifolia				25	0.95*	0.22	179	1.37*	2.07
Prunus serotina				1	1.41	0.01	10	0.92	0.09
Populus grandidentata	14	0.77	0.11	1	0.93	0.01	2	1.12	1.67
Acer rubrum	120	0.66	0.79	207	0.75	1.39			
Amelanchier sp.	4	0.89	0.03						
Quercus rubra	276	0.76*	1.90	2143	1.06*	22.72			
Quercus velutina	1054	0.82	8.79						
Quercus alba	153	0.88	0.88	6	1.00	0.06			
Pinus strobus	5	0.72	0.04						
Pinus resinosa				5	0.71	0.04			
Pteridium aquilinium	4	0.72	0.03						
2. Seeds									
Acer saccharum				13	0.86*	0.29	105	2.29*	2.45
Tilia americana							27	1.49	0.32
Ostrya virginiana				1	2.31	0.02	10	2.41	0.23
Fagus grandifolia							9	1.54	0.14
Quercus rubra	4	0.84	0.03	121	0.86	0.96			
Quercus velutina	115	0.73	0.47						
Ecosystem Mean[1]									
Litter Weight	1749 a			3179 b			2624 b		
Total N			13.1 a			30.5 b			32.5 b

[1] Fisher's protected LSD was used to compare ecosystem means. Means in a row with the same letter are not significantly different at an alpha = 0.05.

* Stand means are significantly different at alpha = 0.05 and were compared using a t-test.

maple (*Acer saccharum* Marsh.) litter represented a much smaller proportion of total litterfall in the sugar maple-red oak/*Maianthemum* stand (20%), whereas red oak (*Quercus rubra* L.) accounted for 68% of the total litterfall. Red oak was much less important in the black oak-white oak/*Vaccinium* stand, where black oak (*Quercus velutina* Lam.) accounted for 63% of the litterfall. Seeds formed only a minor proportion of total litterfall in all stands.

Stand means for N content (kg/ha N) followed a trend similar to total litterfall (Table 2.2). The N content of litterfall in the sugar maple-basswood/*Osmorhiza* stand was 31.9 kg/ha N and 30.4 kg/ha N in the sugar maple-red oak/*Maianthemum* stand; means were not significantly different. The total amount of N returned to the forest floor in the oak stand was 13.5 kg/ha and was significantly lower than in both northern hardwood forests (Table 2.2).

Litter N concentrations (%) for an individual species occurring in several ecosystems was often different. Sugar maple, basswood and beech litter had significantly higher concentrations of N in the sugar maple-basswood/*Osmorhiza* forest compared to the sugar maple-red oak/*Maianthemum* forest. The same is true for the N concentration of sugar maple seeds (Table 2.2). Red oak litter had significantly greater total N (39% more) in the sugar maple-red oak/*Maianthemum* forest compared to the black oak-white oak/*Vaccinium* forest (Table 2.2). Other species common to more than one ecosystem did not have significantly different N concentrations.

Discussion

Community composition, structure and rates of potential N turnover displayed a consistent pattern over the landscape we studied. At the spatial scale of our study, composition and structure of the plant community were strongly related to landform and soil. Principal component analysis confirmed patterned variation in the ground-flora composition which corresponded to variation in the moisture holding capacity of the soil. In the Lake States, there is a significant correlation among landform, soil and vegetation (Barnes et al. 1982; Pregitzer and Barnes 1982; Pregitzer et al. 1983; Pregitzer and Barnes 1984; Pastor et al. 1984; Spies and Barnes 1985; Host 1987).

Potential N turnover was strongly related to species composition of the ecosystem. This relationship undoubtedly arises from differences in the chemical quality of plant litter which, in turn, is the substrate for mineralization. Other factors such as P availability, which we did not measure, may also contribute to this relationship (Pastor et al. 1984).

Nitrification was most important in the sugar maple-basswood/Osmorhiza ecosystem, where 51% of the total N mineralized was oxidized to NO_3^--N. Mineralization was also highest in this ecosystem and seems to be related to the high concentration of total N within the plant litter. Nitrification was unimportant in the black oak-white oak/Vaccinium ecosystem, where only 2% of the mineralized N was converted to NO_3^--N. Pastor et al. (1984) reported that changes in mineralization and nitrification across a moisture gradient were related to species replacement. Our results support their findings.

Vitousek (1982) proposes that forest trees tend to translocate small amounts of N out of leaf tissue prior to abscission in ecosystems which cycle N rapidly. As the rate of intraecosystem N cycling declines, the relative amount of N translocated out of leaf tissue prior to abscission increases. Our results suggest that the black oak-white oak/Vaccinium oak ecosystem is cycling much less N in autumn litterfall compared to the northern hardwood forests. Perhaps the uniform production of lower quality litter, which blankets the forest floor, is why there is less spatial variation in mineralization in the black oak-white oak/Vaccinium ecosystem. Ninety-four percent of the litter in this forest was oak leaves and seeds.

It is important to point out that the incubation we used is an estimate of "potential" N mineralization and nitrification. The rate of NH_4^+ and NO_3^- production observed in the laboratory may not reflect production in the field. Because of sieving, carbon limitations may be temporarily reduced. Substrate availability must have a large impact on N transformations since soil microorganisms are carbon limited (Grey and Williams 1971). Therefore, mineralization may be over-estimated in samples which have been processed in this manner.

A second factor which influences N transformations under laboratory conditions is the exclusion of plant roots. In the field roots compete for inorganic N. Removing root competition probably provides a larger pool of available NH_4^+-N for nitrifying bacteria. Therefore, nitrification may be over-estimated when roots are excluded. The black oak-white oak/*Vaccinium* ecosystem, however, exhibited very low amounts of potential mineralization and nitrification even under laboratory conditions conducive to these processes. Obviously, root competition and temporary changes in carbon availability are not the only factors influencing N dynamics.

There was an apparent relationship between the diversity of the ground flora community and amounts of potential nitrification. The spring ephemeral community was best developed in the sugar maple-basswood/*Osmorhiza* ecosystem, where nitrification was highest. Members of the ephemeral community were totally absent in the oak ecosystem and poorly represented in the sugar maple-red oak/*Maianthemum* ecosystem.

The majority of scientific knowledge concerning the dynamics of intraecosystem N cycling has been developed on a point-specific basis. That is, forest communities which differ in composition have been compared by studying a single stand in each community type. Our study differed in that floristically different ecosystems were spatially replicated over the landscape. Our results suggest that the relationship between species composition and N turnover can be extended across the landscape. Ecosystems that repeatedly occur in different landscape positions with characteristic soils and species composition will likely exhibit a concomitant pattern in N turnover. It appears possible to link landscape patterns with point-specific process level studies. Such links are important because we manage landscapes, not points. Understanding patterns of landform, soil and vegetation across local and regional landscapes should better enable managers to predict the response of ecosystems to natural changes and management treatments.

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Chapter III

SPATIAL PATTERNS OF INTRAECOSYSTEM NITROGEN CYCLING

Abstract

Net N mineralization and nitrification were studied in three forest ecosystems that differed in species composition and structure to gain an understanding of the spatial and temporal dynamics of N turnover. The upland forests studied were two sugar maple ecosystems that differed in ground flora composition and an oak ecosystem. Sampling three stands in each ecosystem type provided spatial replication across a two county area in northwestern Lower Michigan. Aboveground woody biomass and mean annual biomass increment were estimated using species-specific allometric biomass equations. Net N mineralization and nitrification were determined by an *in situ* buried polyethylene bag technique in which surface soil samples were incubated at monthly intervals for one year. Litter was collected during autumn in each ecosystem from one randomly selected stand.

Distinct patterns of overstory production, N mineralization and nitrification were present across the upland landscape and were related to the spatial distribution of ecosystem types. Aboveground woody biomass and its allocation to annual increment increased across the ecosystem

gradient with the lowest values measured in the xeric oak ecosystem and the greatest values in the sugar maple-basswood/*Osmorhiza* ecosystem. Net annual N mineralization estimated from the buried bags was 86.1 kg ha^{-1} yr^{-1} in the oak ecosystem and was significantly less than annual mineralization in the two sugar maple ecosystems. Mineral N production was equivalent in the sugar maple-basswood/*Osmorhiza* and sugar maple-red oak/*Maianthemum* ecosystems; values were 107.0 and 105.2 kg ha^{-1} yr^{-1}, respectively. Annual nitrification was greatest in the sugar maple-basswood/*Osmorhiza* ecosystem where 82% of all mineral N was oxidized to nitrate (88.1 kg ha^{-1} yr^{-1}). Nitrification was minimal in the oak forest; totaling only 5% of annual mineralization. Temporal patterns of available NO_3^-, N mineralization and nitrification were pronounced in the sugar maple-basswood/*Osmorhiza* forest where intraecosystem N cycling was most dynamic. The spatial distribution of forest ecosystems could be used to predict landscape patterns of N mineralization and nitrification. Nitrate loss following intensive forest management practices seems more probable in the sugar maple-basswood/*Osmorhiza* ecosystem, which occurs on the finer-textured moraines throughout northwestern Lower Michigan.

Introduction

Forest ecosystems are dynamic entities changing in both time and space. Ecologists have long sought to identify the biotic and abiotic factors which regulate the spatial distribution of forest ecosystems. Curtis (1959) in a gradient analysis of Wisconsin, determined that climate and soils impart an important influence on the demography of species and forest communities. Later, Peet and Loucks (1977) obtained similar results in southern Wisconsin and included soil nutrients as another important variable. In Michigan, ecosystem classification studies have demonstrated that the spatial distribution of forest communities was integrally linked to landscape patterns of physiography and soil (Pregitzer and Barnes 1982, 1984). Other research has focused on understanding factors affecting temporal changes in forest composition and structure (Olsen 1958; Peet and Christensen 1980; Abrams et al. 1985; McCune and Cottam 1985).

The fundamental environmental constraints directing spatial and temporal changes in forest composition and structure are relatively well established. However in a comparative sense, we know little about how functional ecosystem properties, such as intraecosystem N cycling, change across space and through time. Several studies have detailed seasonal or successional changes in the flow of N within forests (Montes and Christensen 1979; Lamb 1980; Robertson and Vitousek 1981; Robertson 1982; Nadelhoffer et al. 1982; Pastor et al. 1984). However, spatial patterns of intraecosystem N cycling, akin to landscape patterns of forest composition and structure, remain relatively undefined. Most N cycling studies have been point-specific: we know little about landscape variability and cannot predict rates of N turnover across regional and local landscapes.

The ability to extrapolate point-specific processes across regional or local landscapes is of fundamental importance. For example, foresters typically alter intraecosystem fluxes of N by harvesting and site preparation treatments at the scale of 10 to 100 hectares. We know a great deal regarding the microbiology and even enzymology of the processes regulating NO_3^- loss in forested ecosystems. However, we lack the conceptual and empirical foundation that facilitates the spatial extension of this information across large land areas. The primary aim of this study was to understand spatial and temporal patterns of N mineralization and nitrification by integrating factors that influence both ecosystem development and N turnover.

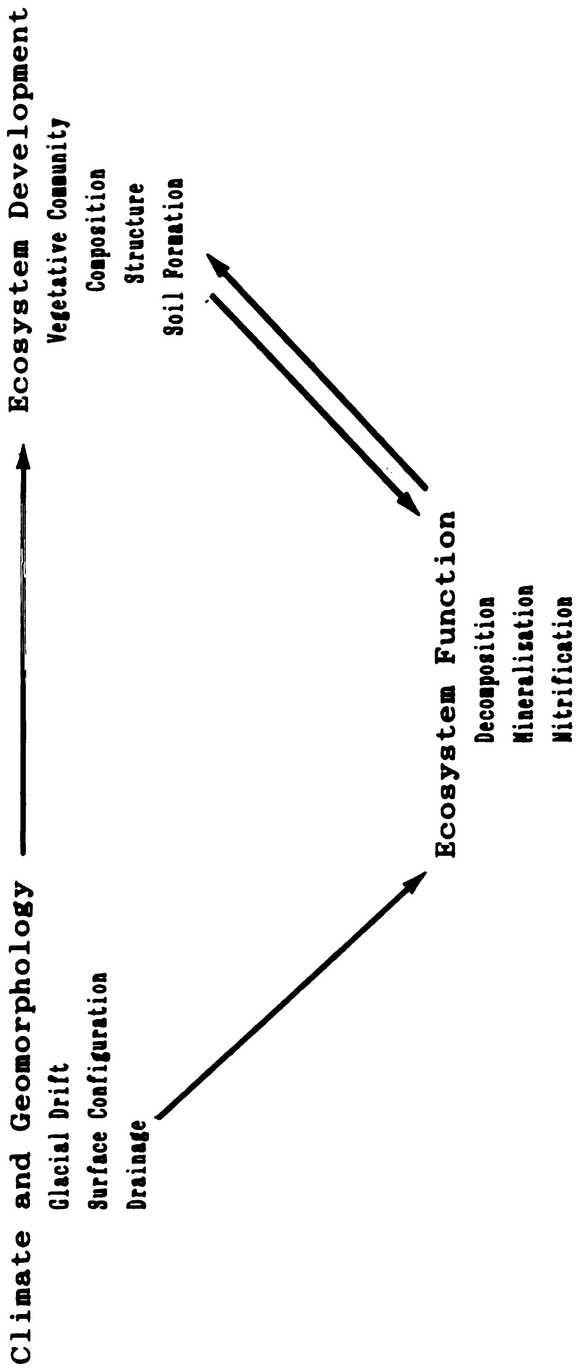
Spatial Patterns of Intraecosystem N Cycling: A Conceptual Model

Nitrogen cycling within forest ecosystems is regulated by a complex interrelationship involving plant uptake, the quantity and chemical composition of plant litter returned both above and below ground, the mineralization of organic material through the activities of soil microorganisms, and nitrification. This relationship is thought to be highly coordinated through plant nutrient use efficiencies, which directly influence the chemical composition of plant litter (Vitousek 1982). In turn, available moisture is believed to have influenced the evolution of plant nutrient use efficiency, since species occupying xeric sites are often efficient in the use of both water and nutrients (Monk 1966; Vitousek 1982).

The rate and quantity of N available for plant growth in temperate forests is largely determined by the process of mineralization, the microbial liberation of NH_4^+ from organic compounds. In turn, the rate at which plant material is mineralized is regulated by its chemical recalcitrance (Aber and Melillo 1982; Melillo et al. 1982) and P content (Chapin et al. 1978; Pastor et al. 1984). Soil moisture influences N mineralization by regulating i) the activities of soil microorganisms and ii) plant nutrient use effiencies which directly control litter quality (Vitousek 1982). Therefore, intraecosystem N cycling is coordinated through biological processes operating under climatic and geomorphological constraints, two physical constraints which ultimately determine moisture availability.

Our conceptual model describing the spatial dynamics of intraecosystem N cycling is centered on the hypothesis that moisture availability is a key environmental factor influencing ecosystem development, N accrual through time and N turnover, at least within the Lake States (Figure 3.1). Here the distribution of forest ecosystems is related to physiography and soil, which directly determine site moisture availability within the local landscape (Pregitzer and Barnes 1984). Pastor et al. (1984) found that rates of N mineralization were related to particular overstory assemblages which, in turn, were a function of a moisture-edaphic gradient. Recently, differences in potential N mineralization and nitrification were found to parallel changes in community composition and structure (Chapter II). Spatial and temporal patterns of N turnover should correspond to landscape patterns of community composition, since soil moisture directly influences community composition, litter quality and N mineralization. Pastor and Post (1986) included these variables in a simulation model predicting successional patterns of C and N cycling. We hypothesized that spatial and temporal patterns of N mineralization and nitrification coincide with the spatial distribution of forest ecosystems within a regional landscape. We tested our hypothesis and conceptual model by comparing net N mineralization and nitrification among three upland forests widely distributed across northern Lower Michigan.

Figure 3.1. A conceptual model describing the spatial distribution of forest ecosystems within glacial landscapes. The model links patterns in landform, soil, community compostion, N mineralization and nitrification.


Climate and Geomorphology
Glacial Drift
Surface Configuration
Drainage
Ecosystem Development
Vegetative Community
Composition
Structure
Soil Formation
Ecosystem Function
Decomposition
Mineralization
Nitrification

Methods

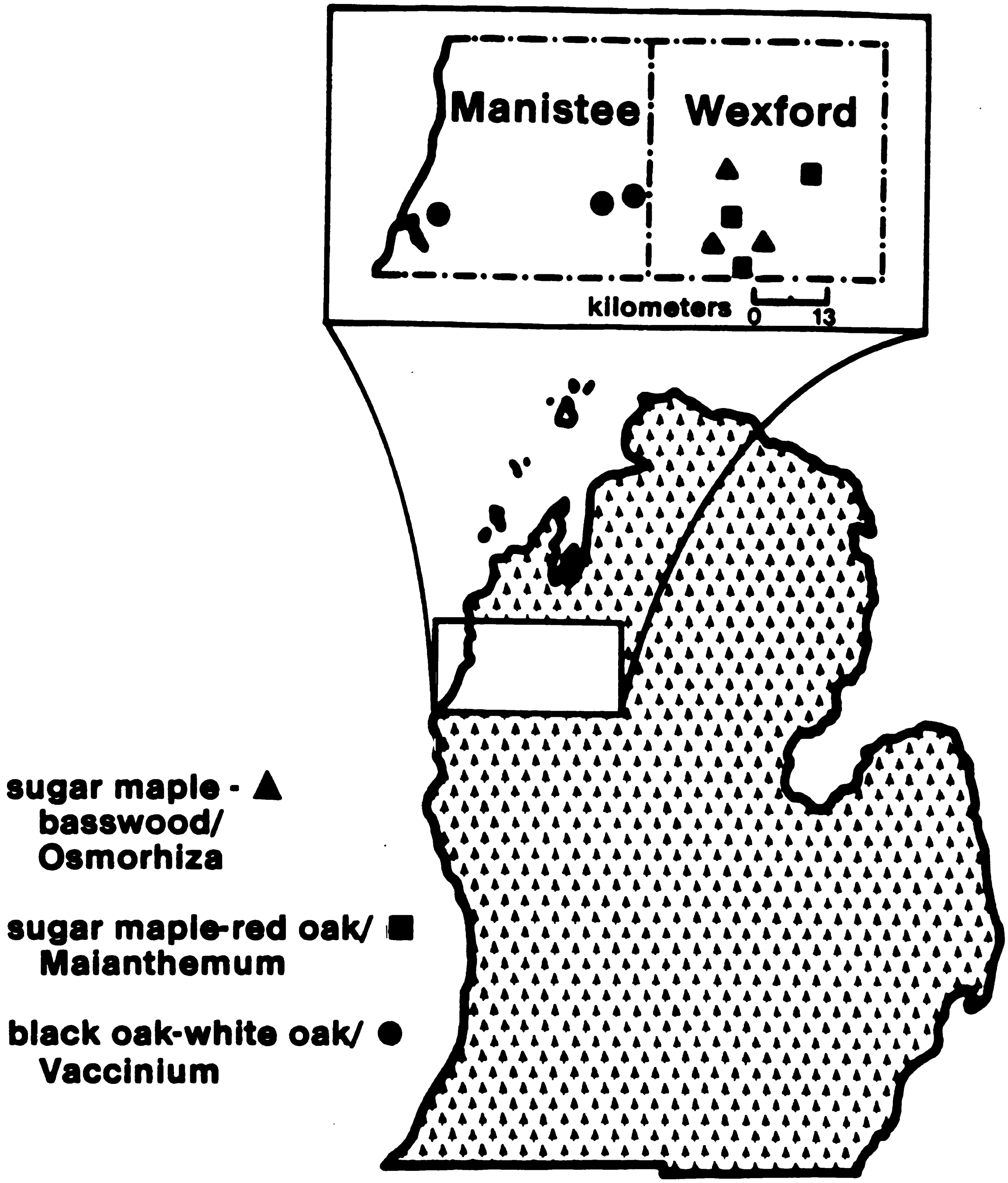
Study Area

Our study was conducted in the upland portions of Manistee and Wexford Counties, northwestern Lower Michigan, Latitude 44° 48' N, Longitude 85° 48'W (Figure 3.2). Mean annual temperature is 7.2° C and the length of the growing season varies from 150 days near Lake Michigan, in the western portion of the study area, to 100 days 60 km inland. Precipitation is evenly distributed through out the year and mean annual precipitation totals 81 cm (Albert et al. 1986).

The present landscape, formed by the last glacial advance approximately 12,000 years BP, is a mosaic of well sorted outwash plains, pitted ice-contact features, sandy till plains and moraines (Ferrand and Eschman 1974). The Interlobate moraine, which transects northern Wexford County, is a predominant landscape feature and has the highest elevation in the study area, 335 m above sea level. Organic-rich quartzitic sands and gravel compose this morainal system and soils are Typic Haplorthods. Northern hardwood forests typify the Interlobate moraine and are some of the most productive forests in the region (Host 1987).

The Port Huron moraine extends into northern Manistee County and is also composed of sandy glacial drift. Soils occurring on this landform are similar to the Interlobate

Figure 3.2. The distribution of study sites within three upland forest ecosystem types in Manistee and Wexford Counties, northwestern Lower Michigan. Stands were separated by a minimum distance of at least 6 km.


Manistee
Wexford
kilometers 0 13
sugar maple - ▲ basswood/ Osmorhiza
sugar maple-red oak/ ■ Maianthemum
black oak-white oak/ ● Vaccinium

moraine. The Port Huron moraine is dominated primarily by red oak (Quercus rubra L.) and white oak (Quercus alba L.) rather than northern hardwoods. This difference may be related to the fire history of the area (Host 1987). A network of well sorted outwash plains dominate the landscape in southern Manistee County. Typic Udipsamments have developed in the more xeric portions of these outwash plains, while Entic Haplorthods have formed where conditions are more mesic; both soils are derived from well sorted medium sands. Forests of the outwash plains were dominated by black oak (Quercus velutina Lam.) and white oak (Quercus alba L.) and by upland pin oak (Quercus ellipsoidalis Hill) where conditions were slightly more xeric.

At the turn of the century, large portions of Manistee and Wexford Counties were commercially logged for eastern white pine (Pinus strobus L., Mustard 1983). This activity seems to be restricted to the xeric portions of the morainal systems and to the outwash plains; decomposing eastern white pine stumps are common there (personal observations). The northern hardwood forests, which are somewhat younger than the forests currently on the outwash plains, may have been logged at a later date; the oldest northern hardwood stands established circa 1920.

Vegetation, soil and forest productivity data were collected during 1983 from 58 stands within the study area (Host 1987). Stands were one hectare or larger and exhibited no evidence of recent disturbance. Stands were classified into ecosystems using an integrated classification approach (Barnes et al. 1982; Pregitzer and Barnes 1984; Spies and Barnes 1985). Three upland forest ecosystems were chosen for this study: two sugar maple ecosystems that differed in ground flora composition and an oak ecosystem (Chapter II). Three stands in each ecosystem were randomly selected from the pool of 58 previously sampled stands. The stratified random sampling scheme provided spatial replication of the ecosystems across the two county study area (Figure 3.2).

The three ecosystems we studied were: black oak-white oak/*Vaccinium*, sugar maple-red oak/*Maianthemum* and sugar maple-basswood/*Osmorhiza*. The names used are convenient abbreviations for the classification units and connote more than just plant communities. They represent integrated landform, soil and vegetation units (Barnes et al. 1982). These ecosystems repeatedly occur across thousands of hectares in northern Lower Michigan. They also represent a moisture-edaphic gradient with the sugar maple-basswood/*Osmorhiza* forest consistently found on mesic sites in the Interlobate moraine. The sugar maple-red oak/*Maianthemum* forests occurred on the drier, but still mesic portions of the Interlobate moraine, while the black oak-white oak/*Vaccinium* ecosystem typically occurred on the xeric portions of the Port Huron moraine and outwash plains. Principal component analysis has demonstrated that the ground flora communities within these forests were distinct (Chapter II).

Vegetation and Soil Analysis

In each stand, four 5 x 30 meter plots were randomly located for soil and vegetation sampling. Overstory trees (dbh greater than 10 cm) were measured using a 10 BAF (English) point sample located at the center of each plot. Diameter (dbh) and total height were measured for each tally tree.

Plant litter was collected during September and October 1984 in one randomly selected stand in each ecosystem. Ten litter traps were randomly located among the four plots in each stand. Litter was collected at 3 week intervals from the 250 cm^2 traps and returned to the laboratory where it was oven dried at 80^{o} C for 24 hours. The dried litter samples were weighed to determine autumn litterfall on an areal basis. Each sample was then ground in a Wiley mill and digested with concentrated H_2SO_4 and K_2SO_4 - HgO as a catalyst in a block digestor. The digestate was analyzed for total N using a Technicon Autoanalyzer II (Technicon 1977). Plant nutrient use efficiency was calculated as the weight of plant litter per unit of total N (Vitousek 1982). A detailed analysis of litterfall components is presented in Chapter II.

Net N mineralization and nitrification were determined by an *in situ* buried polyethylene bag technique (Eno 1960; Ellenberg 1974; Pastor et al. 1984). Soil samples were incubated in four 30 meter transects randomly located within each stand; one transect within each 5 x 30 meter plot. Six samples were incubated along each transect, totaling 24 incubations per stand. Soil samples consisted of a core 100 cm^2 and 3.8 cm in depth taken from below the loose litter. Therefore, samples were incubated in the Oe and A horizons in the oak stands and in the A horizon in the sugar maple stands. Samples were removed from the surface soil, placed undisturbed into polyethylene bags (0.01 mm thick), sealed, returned to their original position in the horizon and the litter was replaced. A second paired sample was taken adjacent to each incubation to determine initial NH_4^+-N and NO_3^--N concentrations. Samples were incubated for one month intervals; except during winter when samples were incubated for 4 months due to heavy snow cover. The incubation transect was moved laterally across the 5 x 30 meter plot with each successive sampling. No incubations were initiated until at least 24 hours after rainfall.

At the termination of the experiment, twenty-four additional soil samples were collected to determine bulk density, pH and organic-C. One sample was collected at a 50 cm depth in each plot and composited on a stand basis for textural analysis. The total content (380 cm^3) of each surface sample was oven-dried at 100° C and weighed to determine bulk density (g/cm^3). Soil pH was determined by a 1:1 soil to deionized water paste (McLean 1982). Organic-C was determined by the Walkley-Black method (Walkley 1947) and B horizon silt + clay was determined by wet seiving.

After collection, initial and incubated samples were refrigerated and returned to the laboratory for analysis. Samples were stored at 2° C until they could be processed, usually within 10 days following collection. Optimally, samples should be processed immediately following collection. However, the large number of samples, 432/month, precluded immediate analyses. Random subsamples, two from each plot, were taken prior to storage to determine if the lag between collection and extraction affected NH_4^+-N and NO_3^--N concentrations.

Field moist samples were sieved and material greater than 2 mm was excluded. A 10 g subsample was extracted with 20 ml of 2 N KCl and a second 10 g subsample was oven-dried at 100° C for 24 hours to determine oven-dried weight. A Technicon Autoanalyzer II was used to determine NH_4^+-N and NO_3^--N in the extraction filtrate. Color development with Na-phenolate was used to determine NH_4^+-N and Cd reduction followed by color development with n-napthylethylene diamine was used to determine NO_3^--N (Technicon Instruments 1977; Technicon Instruments 1978).

Net nitrogen mineralization was determined as the increase in NH_4^+-N plus NO_3^--N in incubated samples in excess of initial concentrations. Similarly, net nitrification was determined as initial NO_3^--N concentrations subtracted from concentrations after incubation. Bulk density was used to convert nutrient concentrations to a weight per unit area basis (kg/ha). Samples incubated over winter (4 months) were expressed as monthly means. Net mineralization and nitrification data were summed over the nine sampling dates to determine the net flux of mineral N and NO_3^--N per annum.

Statistical Analysis

Tree tally data were converted to areal aboveground woody biomass estimates using BIOMASS, an interactive micro-computer program developed at the Forest Ecology Laboratory, Michigan State University (Host 1987). Aboveground woody biomass was calculated using species specific allometric biomass equations developed for Lake States hardwoods. Mean annual biomass increment (t ha^{-1} yr^{-1}) was calculated as the mean total aboveground woody biomass divided by mean plot age (Host 1987).

Temporal mineralization and nitrification data were analyzed using an analysis of variance (ANOVA) procedure for a nested model (ecosystem; stands within ecosystem) with date interactions (SAS 1982). Other data, such as annual mineralization, annual nitrification and total biomass, were analyzed using a nested analysis of variance (SAS 1982). Means were compared using a protected Fisher's LSD procedure with significance accepted at alpha = 0.05. Concentrations of NH_4^+-N and NO_3^--N in immediately processed and stored samples were compared using a t-test for paired observations.

Results

Vegetation

Overstory structure and production varied significantly among the upland forests. Age and the number of stems did not significantly differ among ecosystems (Table 3.1). However, aboveground woody biomass exhibited a significant trend with the smallest quantities present in the oak ecosystem. Aboveground biomass was greatest in the sugar maple-basswood/Osmorhiza ecosystem (206.8 t/ha). Mean annual biomass increment displayed a significant and identical trend. Aboveground biomass increment peaked in the sugar maple-basswood/Osmorhiza forest (3.27 t ha^{-1} yr^{-1}). Litter production (kg/ha) and the quantity of total N returned in litterfall differed among the upland forests with the sugar maple ecosystems returning significantly greater quantities of litter compared to the oak ecosystem. In general, litterfall and total N contents were approximately double in the sugar maple forests (Table 3.1). Nutrient use efficiency declined across the ecosystem gradient. Of the

Table 3.1 Selected overstory and soil properties for three upland forest ecosystems. Values represent the mean (standard deviation) of three stands within each ecosystem. Means within a row that have the same letter are not significantly different at alpha = 0.05.

	black oak-white oak/ *Vaccinium*	sugar maple-red oak/ *Maianthemum*	sugar maple-basswood/ *Osmorhiza*
	Ecosystem Means		
I. Overstory			
Age (yrs)	71a (16.1)	64a (4.2)	63a (9.6)
Trees/ha	864a (576)	761a (329)	790a (353)
Aboveground Biomass (tons/ha)	151.2a (52.27)	177.9ab (42.21)	206.8b (38.88)
Mean Annual Biomass Increment (tons ha^{-1} yr^{-1})	2.25a (0.97)	2.80ab (0.62)	3.27b (0.89)
Litterfall (tons/ha)	1.75a (0.83)	3.18b (0.61)	2.62b (0.72)
Litterfall N (kg/ha)	13.1a (1.23)	30.4b (2.36)	32.5b (1.98)
Nutrient Use Efficiency	133	104	82
II. Soil			
A. 0 to 3.8 cm			
pH	3.89a (0.05)	4.06a (0.13)	5.59b (0.15)
Organic-C (%)	4.4a (1.18)	3.9a (1.27)	5.5b (2.68)
B. 50 cm			
Silt + Clay (%)	4.0a (0.19)	5.0a (1.77)	8.8b (3.92)

three upland forests, the maple-basswood/Osmorhiza forest had the lowest litter biomass to total N ratio.

Soil Properties

Soil pH and silt + clay increased across the ecosystem gradient. The black oak-white oak/Vaccinium ecosystem had the lowest pH (pH 3.89), but it did not differ from the surface pH of 4.06 in the sugar maple-red oak/Maianthemum ecosystem (Table 3.1). Surface soil pH in the sugar maple-basswood/Osmorhiza forest was 5.59, significantly different from the other two ecosystems. Silt + clay in the B horizon (50 cm) displayed a trend similar to pH (Table 3.1). Most of the uplands of northern Lower Michigan are extremely sandy, so a small change in silt + clay can have important ecological ramifications. Soils within the sugar maple-basswood/Osmorhiza forests averaged 8.77% silt + clay and were the finest textured soils in the study area.

Organic-C differed among the upland forests; the sugar maple-basswood/Osmorhiza forest contained the greatest quantity of organic-C (5.46%). The black oak-white oak/Vaccinium and sugar maple-red oak/Maianthemum ecosystems did not differ in organic-C; quantities were 4.39% and 3.93%, respectively (Table 3.1). The slightly greater organic-C content beneath the oak ecosystem may be attributable to the well developed humus layer which was not present in either sugar maple forests.

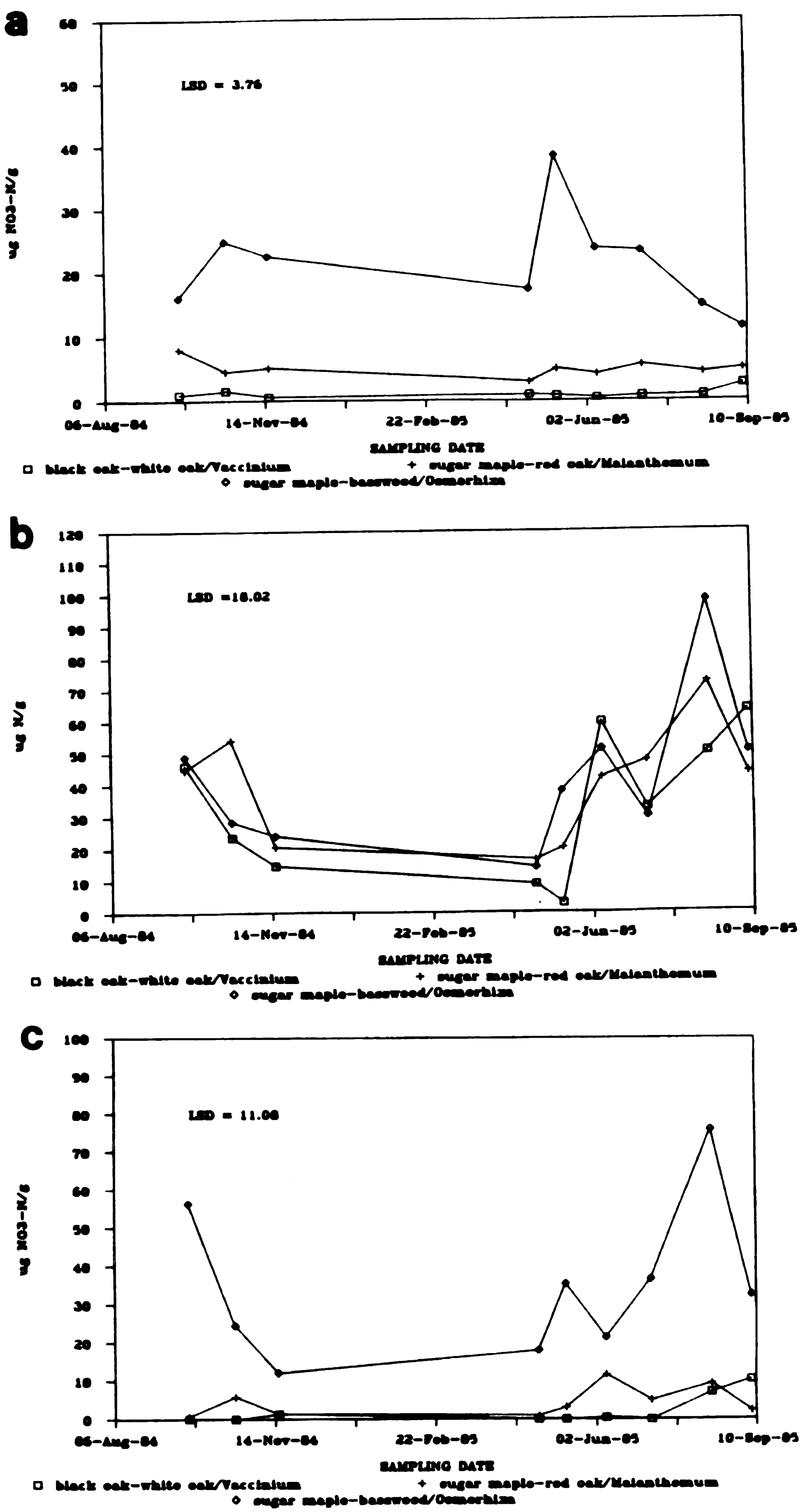
Extractable NO_3^--N

Extractable NO_3^--N at all sampling dates was greater in the sugar maple-basswood/Osmorhiza ecosystem compared to the other ecosystems (Figure 3.3a). Extractable NO_3^--N was minimal in the oak ecosystem with quantities ranging from 0 to 1 ug/g. In general, available NO_3^--N was always greater in the sugar maple-red oak/Maianthemum forest compared to the oak ecosystem, however, differences were not always significant. A weak temporal trend in extractable NO_3^--N was present in the sugar maple-basswood/Osmorhiza ecosystem, but similar trends were not apparent in the other two ecosystems. A large peak in available NO_3^--N occurred in early spring and declined through late spring and summer of 1985. Mean available NH_4^+-N and NO_3^--N in stored and immediately extracted samples were not significantly different using a paired t-test.

Nitrogen Mineralization and Nitrification

Net N mineralization exhibited a pronounced temporal pattern (Figure 3.3b). In general, the black oak-white oak/Vaccinium ecosystem mineralized smaller quantities of N compared to the sugar maple ecosystems. Rates of net mineralization in the two sugar maple ecosystems were equivalent throughout most of the year, however, differences were significant in early fall 1985 (Figure 3.3b). The

Figure 3.3. Extractable NO_3^--N (a), net N mineralization (b), and nitrification (c) in three upland ecosystem types, September 1984 to September 1985.


a
LSD = 3.76
ug NO3-N/g
SAMPLING DATE
06-Aug-84
14-Nov-84
22-Feb-85
02-Jun-85
10-Sep-85
□ black oak-white oak/Vaccinium
+ sugar maple-red oak/Maianthemum
◇ sugar maple-basswood/Osmorhiza
b
LSD =18.02
ug N/g
SAMPLING DATE
□ black oak-white oak/Vaccinium
+ sugar maple-red oak/Maianthemum
◇ sugar maple-basswood/Osmorhiza
c
LSD = 11.08
ug NO3-N/g
SAMPLING DATE
□ black oak-white oak/Vaccinium
+ sugar maple-red oak/Maianthemum
◇ sugar maple-basswood/Osmorhiza

general decline in mineralization present in early spring 1985 may be attributed to increased microbial immobilization resulting from warmer soil temperature and high substrate availability.

Striking differences in nitrification occurred among the ecosystems (Figure 3.3c). Rates of net nitrification, throughout the year, were significantly greater in the sugar maple-basswood/Osmorhiza ecosystem compared to the other ecosystems. Similarly, nitrification was more dynamic in the sugar maple-basswood/Osmorhiza ecosystem. Nitrification was minimal in the black oak-white oak/Vaccinium ecosystem, however, small increases were present in late summer and fall. Rates of net nitrification in the sugar maple-red oak/Maianthemum forest did not significantly differ from those in the black oak-white oak/Vaccinium ecosystem. Temporal changes in nitrification were small in this forest and rates were constant throughout the year.

Net annual fluxes (kg ha^{-1} yr^{-1}) of mineral N displayed a strong trend across the ecosystem gradient (Figure 3.4). Annual net mineralization was 86.1 kg ha^{-1} yr^{-1} in the black oak-white oak/Vaccinium ecosystem and was significantly less than annual mineralization in the two sugar maple ecosystems (Figure 3.4). Mineral N production per annum was equivalent in the sugar maple-basswood/Osmorhiza and sugar maple-red oak/Maianthemum ecosystems; values were 107.0 and 105.2 kg ha^{-1} yr^{-1}, respectively.

A significant and more pronounced trend was apparent in total annual nitrification. The greatest amount of annual nitrification was present in the sugar maple-basswood/Osmorhiza ecosystem where 82% of all mineral N occurred as NO_3^--N (88.1 kg ha^{-1} yr^{-1}). Values in the sugar maple-red oak/Maianthemum and black oak-white oak/Vaccinium forests were significantly lower; 10.7 and 4.5 kg ha^{-1} yr^{-1}, respectively (Figure 3.4). Although annual fluxes of mineral N were equivalent in the sugar maple forests, NH_4^+-N had two different fates. In the sugar maple-red oak/Maianthemum ecosystem 89% of the mineral N remained as NH_4^+-N whereas only 18% remained as NH_4^+-N in the sugar maple-basswood/Osmorhiza ecosystem. Nitrification was minimal in the oak ecosystem where only 5% of the mineral N was oxidized to NO_3^--N.

Mean rates of annual mineralization and nitrification for individual stands are presented in Figure 3.5. With the exception of one stand, there was no overlap between stands from differing ecosystem types. Annual mineralization formed a continuum from the lowest values in the oak stands to the highest in the sugar maple-basswood/Osmorhiza stands. Stands within the sugar maple-red oak/Maianthemum and black oak-white oak/Vaccinium ecosystem did not differ significantly in annual mineralization. However, one stand (Stand 6) in the sugar maple-basswood/Osmorhiza ecosystem mineralized much

Figure 3.4. Mean annual net N mineralization and nitrification for three upland forests, September 1984 to September 1985. Means with the same letter are not significantly different at alpha = 0.05.

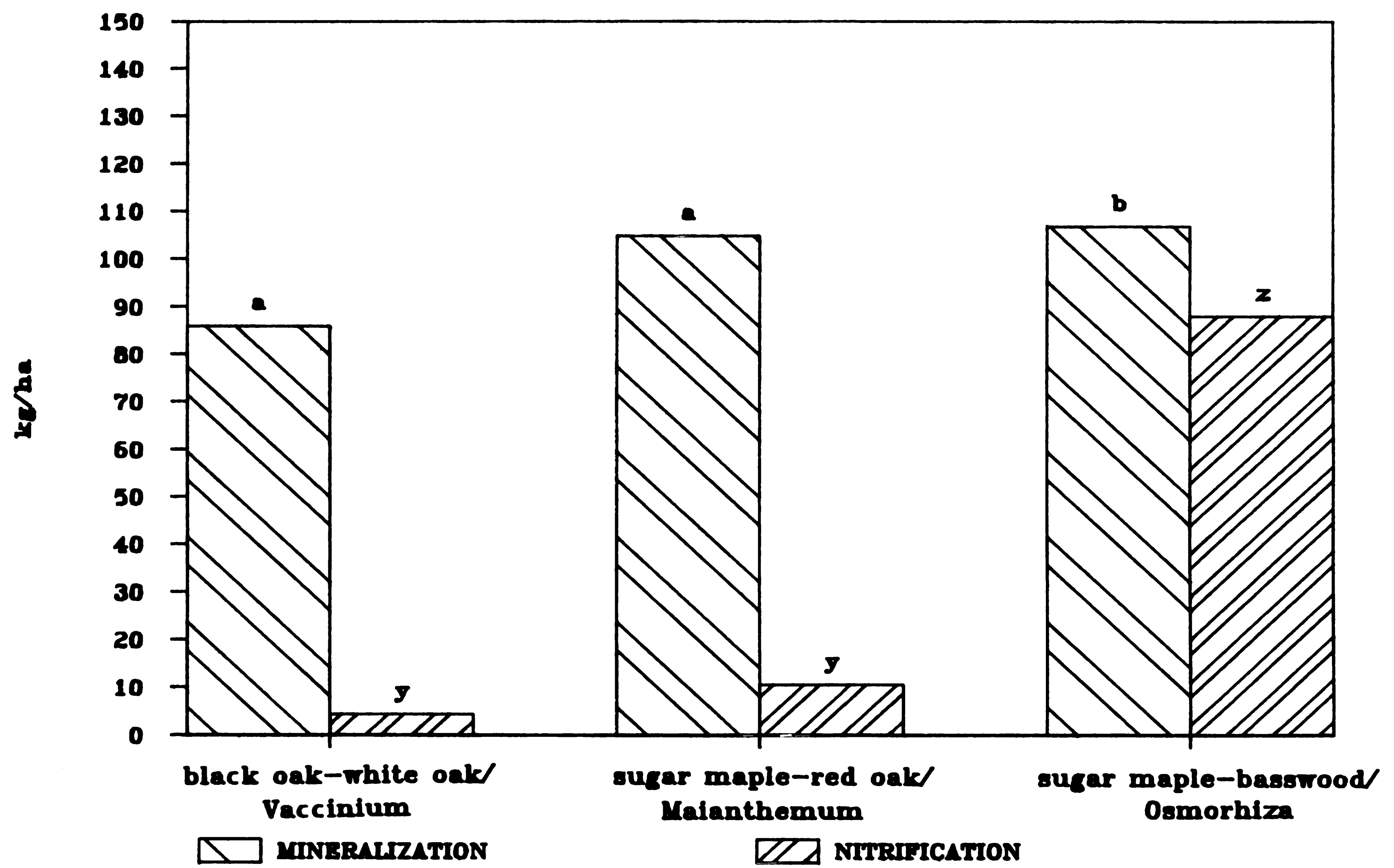
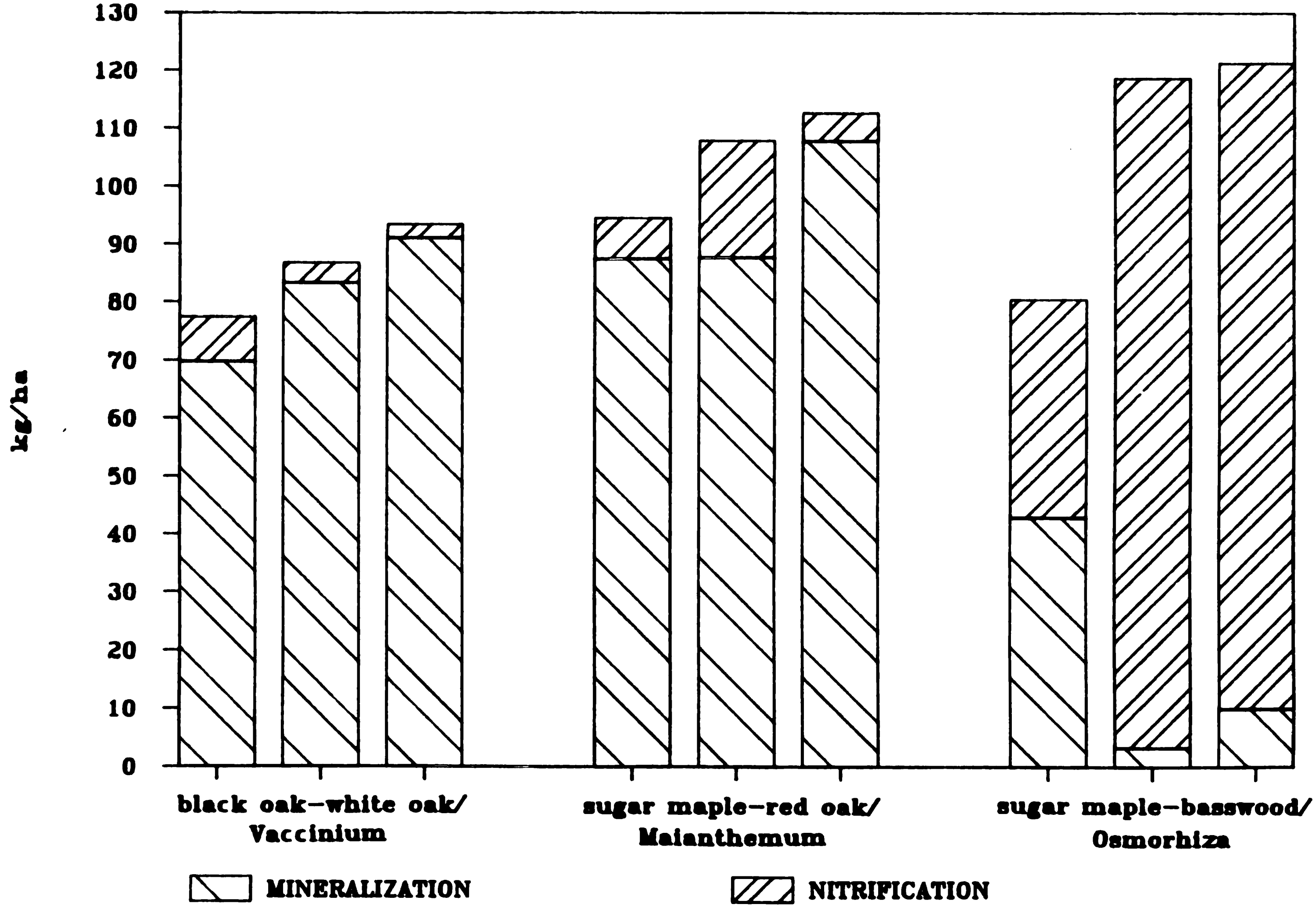

kg/ha
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
a
y
a
y
b
z
black oak–white oak/
Vaccinium
sugar maple–red oak/
Maianthemum
sugar maple–basswood/
Osmorhiza
MINERALIZATION
NITRIFICATION

Figure 3.5 Mean annual net N mineralization and nitrification for individual stands within each ecosystem type. Annual N mineralization is represented by the total length of each bar.


130
120
110
100
90
80
70
60
50
40
30
20
10
0
kg/ha
black oak-white oak/
Vaccinium
sugar maple-red oak/
Maianthemum
sugar maple-basswood/
Osmorhiza
MINERALIZATION
NITRIFICATION

lower quantities of N than did the other stands (Figure 3.5). In general, nitrification increased across the landscape gradient. However, one sugar maple-basswood/Osmorhiza stand had significantly lower net annual nitrification compared with the other two stands in this ecosystem type.

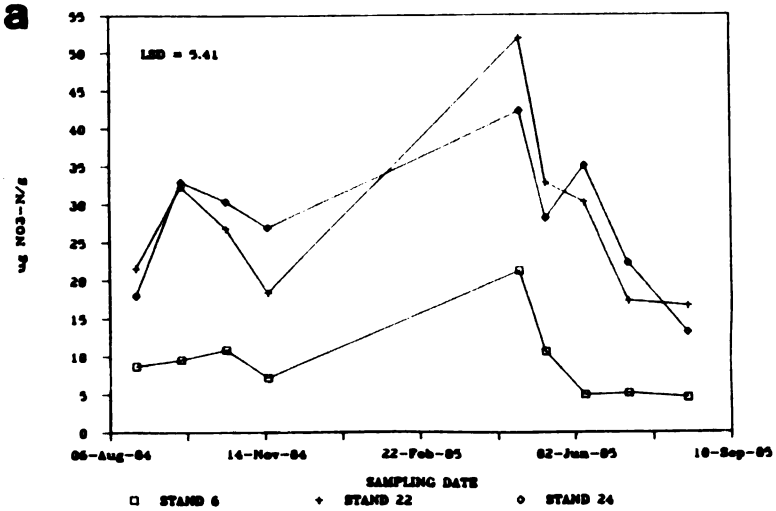
Anomalies in the sugar maple-basswood/Osmorhiza Ecosystem

The differences present among the three sugar maple-basswood/Osmorhiza stands were not consistent with the overall trends in mineralization and nitrification. The differences reported here were also present in a companion study that assayed potential mineralization and nitrification by aerobic laboratory incubation (Chapter II). Floristically and edaphically these three stands were similar, but annual nitrogen turnover was quite different. Total mineralization was 80.7 kg ha^{-1} yr^{-1} in stand 6, the lowest of all stands we studied, and 121.4 and 118.8 kg ha^{-1} yr^{-1} in stands 22 and 24, respectively (Figure 3.5). Throughout the year, consistently lower quantities of available NO_3^--N, net mineralization and nitrification were present in stand 6, compared to stands 22 and 24 (Figure 3.6a). Temporal trends among the stands were similar, but the rate and total quantity of these processes were very different.

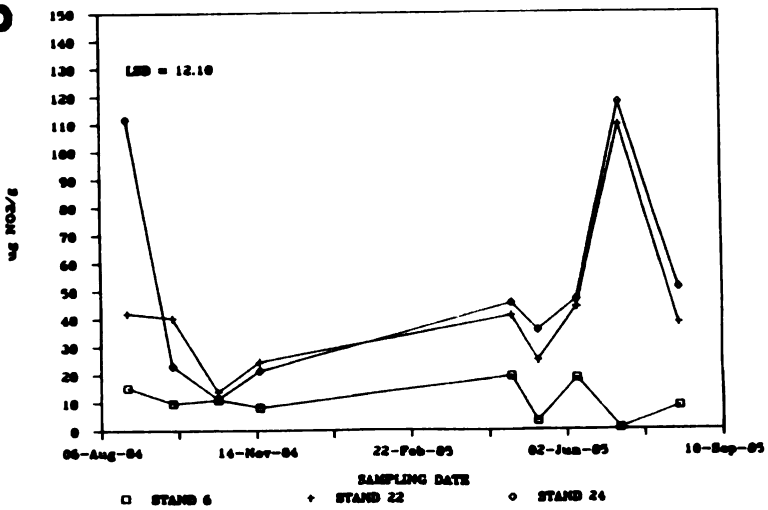
Overstory age, biomass and biomass production were similar among the sugar maple-basswood/Osmorhiza stands

Figure 3.6 Extractable NO_3^--N (a), net N mineralization (b), and nitrification (c) for the three sugar maple-basswood/*Osmorhiza* stands, September 1984 to September 1985.

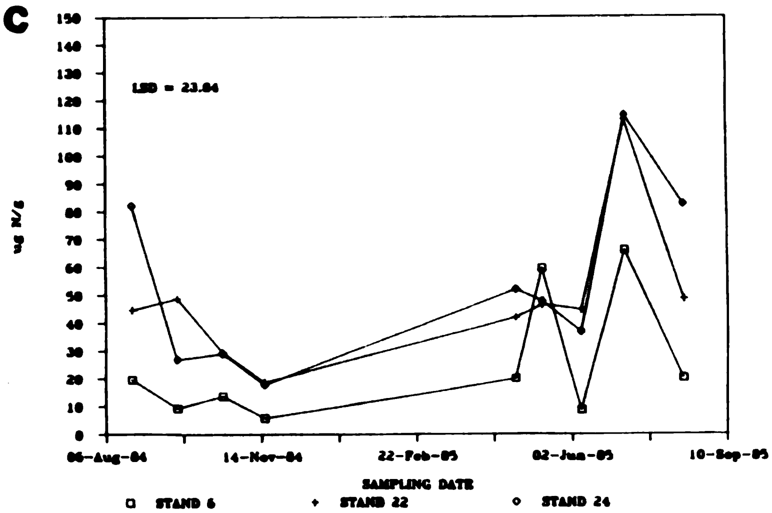
a


LSD = 5.41
ug NO3-N/g
SAMPLING DATE
06-Aug-84
14-Nov-84
22-Feb-85
02-Jun-85
10-Sep-85
STAND 6
STAND 22
STAND 24

b


LSD = 12.10
ug NO3/g
SAMPLING DATE
06-Aug-84
14-Nov-84
22-Feb-85
02-Jun-85
10-Sep-85
STAND 6
STAND 22
STAND 24

c


LSD = 23.84
ug N/g
SAMPLING DATE
06-Aug-84
14-Nov-84
22-Feb-85
02-Jun-85
10-Sep-85
STAND 6
STAND 22
STAND 24

(Table 3.2). Woody biomass and mean annual biomass increment were greatest in stand 6, although not significantly different. It is interesting that stand 6 had the greatest aboveground biomass and mean biomass production, but net annual mineralization was the lowest of the sugar maple-basswood/Osmorhiza stands (Figure 3.5 and Table 3.2).

Soil properties differed among the three sugar maple-basswood/Osmorhiza stands and seem to be related to the differences in N turnover (Table 3.2). Surface soil (0 to 3.8 cm) bulk density was significantly greater in stand 6 (0.88 g/cm^3) compared to stands 22 and 24 where bulk densities were 0.68 and 0.58 g/cm^3, respectively. Organic-C was significantly less in stand 6, approximately one-half the quantity of stands 22 and 24 (Table 3.2). Organic-C was 3.40% in stand 6; and 6.07% and 6.56% in stands 22 and 24, respectively. Net annual mineralization, based as ug N/g soil/yr, displayed an identical trend with annual mineralization; stand 6 mineralized the lowest quantities of N. However, when mineralization was based on the quantity of N mineralized per unit weight of soil organic-C, the substrate for mineralization, no significant differences were present among any of the sugar maple-basswood/Osmorhiza stands (Table 3.2).

Table 3.2. Selected overstory and soil properties for the three sugar maple-basswood/<u>Osmorhiza</u> stands. Means for net N mineralization and nitrification are expressed per unit weight of soil and per unit weight of soil organic-C. Means within a row that have the same letter are not significantly different at alpha = 0.05.

	Stand 6	Stand 22	Stand 24
I. Overstory			
Age	59a	58a	75a
Biomass (t/ha)	229a	165a	226a
Mean Annual Biomass Increment (t ha^{-1} yr^{-1})	3.89a	2.92a	2.99a
II. Soil			
Bulk Density (g/cm^3)	0.88a	0.68b	0.58b
Organic-C (%)	3.4a	6.0b	6.6b
Net Mineralization (ug g $soil^{-1}$ yr^{-1})	241.8a	493.3b	543.9b
Net Mineralization (ug g $organic\text{-}C^{-1}$ yr^{-1})	7112.9a	8127.3a	8291.3a

Discussion

Distinct spatial patterns of overstory production, net N mineralization and nitrification were present across the landscape we studied and were related to the spatial distribution of vegetation and soil. In the Lake States, a significant relationship exists among landform, soil formation and ecosystem development (Barnes et al. 1982; Pastor et al. 1982, 1984; Pregitzer et al. 1983; Pregitzer and Barnes 1982, 1984; Spies and Barnes 1985). In addition, patterns of intraecosystem N cycling coincide with the distribution of forest ecosystems (Pastor et al. 1984; Pastor and Post 1986). The upland forests we studied were floristically distinct (Chapter II), occupied predictable landscape positions, and differed in their spatial and temporal pattern of N turnover.

Spatial patterns of intraecosystem N cycling were integrally linked to forest composition and structure. Annual net N mineralization (kg ha^{-1} yr^{-1}) was represented by a continuum, a pattern which paralleled moisture availability, changes in species composition, and overstory productivity. Mean annual biomass increment, litter production, litter total N, N mineralization and nitrification were lowest in the black oak-white oak/*Vaccinium* ecosystem while the greatest values were measured in the sugar maple-basswood/*Osmorhiza* ecosystem.

Pastor et al. (1984) found that net aboveground production was highly correlated with N mineralization and moisture availability. Our results support their findings and suggest that this relationship can be extended spatially.

Vitousek (1982) suggested that plant nutrient use efficiency is inversely proportional to the quanitity of available N. Therefore, forest trees in N limited environments translocate large quantities of N from their foliage prior to litterfall which results in a high litter biomass:litter total N ratio. The highest nutrient use efficiency we measured was in the black oak-white oak/Vaccinium ecosystem where annual N turnover was lowest. The values reported here (Table 3.1) agree with those of Vitousek (1982) and further support his findings.

Temporal patterns of N mineralization were present among the three upland forests, however, there was considerable variability. Pastor et al. (1984) found maximum daily rates of mineralization occurred during the growing season and became minimal during winter when soil temperatures probably limit microbial activity. This pattern suggests close synchrony between plant uptake and N availability, a pattern also apparent in the forests we studied.

Some of the variability we observed in N mineralization may, in part, be related to the buried polyethylene bag technique. Polyethylene forms an impermiable barrier to water movement and therefore, moisture within the bag remains constant while outside it varies. Net N mineralization may be overestimated during an unusually dry period following incubation. Whereas, underestimations may result during particularly moist periods. These effects may be minimized by shortening the length of incubation which would lessen potential differences within and outside the buried bag.

Available NO_3^--N and nitrification displayed temporal patterns which were most pronounced in the sugar maple-basswood/Osmorhiza ecosystem. The magnitude of temporal fluctuation seems to be directly proportional to rate and pool size. Temporal changes in the available NO_3^--N pools and nitrification were small in the black oak-white oak/Vaccinium ecosystem; rates and pool sizes were consistently small resulting in low annual fluxes. In contrast, large seasonal fluctuations occurred in the sugar maple-basswood/Osmorhiza ecosystem where pools and fluxes were great. Available NO_3^--N pools in this ecosystem type were greater than values reported for most forest ecosystems (Nadelhoffer et al. 1982; Vitousek et al. 1982). Perhaps N cycling is more dynamic in the sugar maple-basswood/Osmorhiza ecosystem simply due to greater N availability.

Nitrification (kg ha^{-1} yr^{-1}) accounted for very different proportions of the annual mineral N pools within the sugar maple forests and was most prevalent in the sugar maple-basswood/*Osmorhiza* ecosystem, where 82% of all mineral N was oxidized to NO_3^--N. In contrast, nitrification consumed only 10% of the annual NH_4^+-N in the sugar maple-red oak/*Maianthemum* ecosystem. These northern hardwood forests were both dominated by sugar maple, however overstory associates differed. Red oak was dominant in the sugar maple-red oak/*Maianthemum* ecosystem; leaves and seeds of this species composed 68% of the litterfall (Chapter II). Oak species were absent in the sugar maple-basswood/*Osmorhiza* ecosystem. Here litter was primarily composed of sugar maple and basswood leaves (Chapter II). Several investigators have reported an inverse relationship between nitrification and the percentage of overstory oak (Pastor et al. 1984). Perhaps the high lignin and low P contents of oak litter in general supress nitrification in the sugar maple-red oak/*Maianthemum* forest (Chase et al. 1968; Purchase 1974; Aber and Melillo 1982; Pastor et al. 1984).

Forest management practices which eliminate plant uptake, such as clearcutting and herbicide application, fundamentally alter intraecosystem N cycling and create the potential for nitrate loss (Bormann et al. 1974; Vitousek 1981, 1982; Vitousek and Melillo 1979; Vitousek et al. 1982; Vitousek and Matson 1985). By defining spatial and temporal patterns of nitrification, we can identify portions of the landscape that have the potential for nitrate loss following disturbance.

Losses seem more probable in the sugar maple-basswood/Osmorhiza ecosystem where available NO_3^--N pools and nitrification were consistently high; particularly in early spring and fall. This forest is relatively common on the heavier-textured moraines throughout Michigan's northern Lower Peninsula. The black oak-white oak/Vaccinium ecosystem occupies thousands of hectares across northern Lower Michigan. Nitrification was minimal, even under optimal laboratory conditions (Chapter II) and clearly, nitrate loss following disturbance is unlikely. The sugar maple-red oak/Maianthemum forests are also very common and, although some nitrification occurred, it appears that nitrate loss is of less consequence compared to the other northern hardwood ecosystem type. Mroz et al. (1985) demonstrated that the impact of intensive harvesting was most severe on high quality hardwood sites, while others (Weetman and Weber 1972; Boyle et al. 1973; Patric and Smith 1975; Jurgenson et al. 1979) have estimated the greatest impacts should occur in unproductive forests. The greatest potential for NO_3^- loss in our study area exists in the most productive portions of the landscape where intraecosystem N cycling is most dynamic.

Spatial and temporal patterns of N mineralization and nitrification are related to the distribution of forest ecosystems at the scale of a regional landscape. In general, rates of N mineralization and nitrification were different among the three upland ecosystems, and with the exception of one sugar maple-basswood/Osmorhiza stand (6), stand means (nested within ecosystem) were not significantly different. We found no evidence to reject our conceptual model outright. In general, there was a strong relationship between the pattern in vegetation and soil and the processes of N mineralization and nitrification.

However, the specific differences among the sugar maple-basswood/Osmorhiza stands support neither our hypothesis or conceptual model. The anomalies among these stands may be related to the pool of organic-C. The microbial substrate for mineralization is organic-C, and quantities of organic-C were low in stand 6. Net mineralization per unit of organic-C did not differ among the sugar maple-basswood/Osmorhiza stands, indicating similar absolute rates. Differences appear to be due to substrate pool sizes and not to differences in the kinetics of mineralization.

Forest floor organic matter pools are known to decline following disturbance such as clearcutting, and aggrade to their pre-disturbance levels after approximately 60 years (Covington 1981; Federer 1984). The sugar maple-basswood/Osmorhiza stands all established approximately 63 years ago and have not been thinned or harvested since (M. Sands, U.S.F.S., personal communication). However, it appears that disturbance was very different in these stands prior to establishment . Evidence of past logging activity (e.g. skid roads and landings) was present in and adjacent to stand 6. Perhaps past disturbance(s) precluded rapid revegetation resulting in increased heterotrophic activity and a reduction in soil organic matter. Although highly speculative, this suggests organic matter dynamics and N cycling may be perturbed for broader time frames than previously thought.

The synthesis of a conceptual model describing the spatial and temporal behavior of intraecosystem N cycling requires the integration of environmentally and biologically important variables that influence not only N turnover, but also influence ecosystem development. Our model is based on the assertion that, in the Lake States, moisture availability is a key environmental factor influencing species composition, soil development and intraecosystem N cycling. Here a parallel pattern exists between community composition and N turnover because: i) the spatial distribution of forest communities are related to climate, physiography and soil (e.g. moisture availability), ii) the chemical constituents of plant litter are directly related to species composition and nutrient use efficiency, and iii) the activities of soil microorganisms, which make N available for plant uptake, are regulated by litter recalcitrance and soil moisture. It is important to note that the conceptual model we developed may not apply to forest ecosystems outside the Great Lakes region or in moist forests where nutrients other than N limit growth. Furthermore, differing patterns of disturbance within an ecosystem type may confound the relationship between species composition and N turnover. Stand 6 seems to be such an example.

We found it possible to link point-specific processes with landscape patterns; these links are important because we manage landscapes, not points. For example, a great deal of effort has been devoted toward understanding mechanisms regulating nitrate loss following disturbance. However, we lack a general model that enables land managers to implement this information. Our results suggest that the relationship between species composition and intraecosystem N cycling can be extended across the landscape and used to provide a general model describing the spatial and temporal dynamics of N turnover. Forest ecosystems with different species composition, structure and growing on different soils will likely exhibit concomitant patterns of intraecosystem N cycling. In northern Lower Michigan, nitrate loss following disturbance seems most probable in the sugar maple-basswood/*Osmorhiza* forests that occurred on the relatively heavier-textured moraines. Nutrient cycling studies conducted from within the framework of an ecosystem classification system can provide a highly utilitarian way of extrapolating N cycling information across regional and local landscapes, particularly since the ecosystems we described can be readily mapped and placed within a regional landscape ecosystem hierarchy (Barnes et al. 1982; Albert et al. 1986).

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Chapter IV

NITROGEN RETENTION BY SPRING EPHEMERAL COMMUNITIES

Abstract

Nitrate reductase (NR) activity was measured in two plant species to determine the mechanism of N retention by spring ephemeral and ground flora communities. Rates of N loss to ground water or denitrification could be slowed through NH_4^+ or NO_3^- uptake. Studies were conducted in a maple - beech and a river flood plain forest that had an abundant coverage of spring ephemeral and herbaceous ground flora species. NR activity was determined for leaf and root tissues of *Allium tricoccum* L. and *Asarum canadense* Ait. by an *in vivo* tissue infusion procedure. Potential net N mineralization and nitrification were determined by aerobic laboratory incubation.

NR activity was low in both species and confined to leaf tissue. Rates of NO_3^- reduction were comparable with those reported for ericaceous species typically associated with habitats where nitrification is minimal. In contrast, potential nitrification was high in both forest types with 99 % of all inorganic N present as NO_3^--N after a 14 week incubation.

Nitrate fertilization was used to induce NR activity in six Asarum canadense clones within each forest. In two separate experiments, deionized water was added to one plot (control) while the second was treated with 60 kg N/ha as NO_3^-. NR activity was significantly greater in fertilized plots. However, induced activities were low and did not significantly contribute to plant N nutrition. Results suggest that Allium tricoccum and Asarum canadense have a limited ability to assimilate NO_3^-. The discrepancy between leaf NR activity and nitrification potential may have resulted from the lack of root competition and stimulation of net mineralization in the laboratory incubation. Alternatively, the NR assay may underestimate NO_3^- assimilation in late successional species. Plant-nitrifier competition may be an important process regulating NO_3^- loss in forested ecosystems and may partially explain the mechanism of the vernal dam.

Introduction

Recently, the distribution of herbaceous species within several Michigan forests was related to high potential rates of N turnover (Chapter II). High laboratory nitrification potentials were related to the spatial distribution of diverse spring ephemeral and herbaceous ground flora communities. Blank et al. (1980) found N uptake by the spring ephemeral community was sufficient to affect system level N fluxes. Nitrogen uptake by the six most abundant species was approximately equivalent to an annual N loss of 6.0 kg/ha (Blank et al. 1980). Development of spring herb communities occurs early in the growing season before the overstory canopy develops and nutrient uptake is substantial. Nitrogen uptake by spring ephemerals has also been proposed as a general mechanism which retains nitrogen at a time when it is likely lost; the ephemeral plants act as a natural "vernal dam" (Muller and Bormann 1978).

The aim of this study was to identify the mechanism of N retention by ground flora. Two different possibilities exist: i) uptake of NO_3^- that would otherwise be lost to ground water or denitrification (i.e. competition between internal and external sinks), and ii) uptake of NH_4^+ before it is nitrified (i.e. competition between plants and nitrifiers). We hypothesized that plant species characteristic of diverse spring ephemeral and herbaceous ground flora communities were adapted to utilize NO_3^-. To evaluate this, nitrate reductase (NR) activity was studied in two plant species particularly important in the ground flora of mesic southern Michigan forests.

Nitrate reductase is an inducible enzyme involved with the first and rate limiting step of NO_3^- assimilation in plants (Bonner and Varner 1976; Beevers and Hageman 1980). Smith and Rice (1983) found a strong relationship between (NR) and NO_3^- availability in an old field sere while others (Bate and Heelas 1975; Haines 1977; Havill et al. 1974) have demonstrated similar relationships in different ecosystem types. We tested our hypothesis by comparing plant NR activity with laboratory nitrification potentials in different late successional forest ecosystems and by attempting to induce NR activity through NO_3^- fertilization.

Methods

A preliminary study and three experiments were conducted to investigate patterns of nitrification and NR activity in herbaceous ground flora. Experiments were conducted on the campus of Michigan State University in Baker Woodlot, a maple-beech forest and the Red Cedar Natural Area, a river flood-plain forest dominated by *Acer saccharum* Marsh. and *Acer nigrum* Michaux f. The ground flora of both sites was dominated by *Allium tricoccum* L., a spring ephemeral and *Asarum canadense* Ait., which was present throughout the growing season (Plate 4.1). These species represented a significant proportion of herbaceous biomass within both forests.

Nitrate Reductase Assay

Potential N mineralization and nitrification were determined by aerobic soil incubations (Vitousek et al. 1982). Soil samples were collected within both forests (July 1984) from 10 random locations to a depth of 10 cm. A 10 g subsample of sieved soil was extracted with 2 N KCl and analyzed for NH_4^+-N and NO_3^--N with a Technicon Autoanalyzer II. NH_4^+-N was determined by color development with Na-phenolate (Technicon 1977). Cadmium reduction followed by color development with n-napthylethylenediamine was used to determine NO_3^--N (Technicon 1977). A total of 110 subsamples were incubated at 30° C, 80% relative humidity and maintained at field capacity by daily addition of deionized water. Ten subsamples were analyzed weekly for six weeks, after which, the remaining samples were analyzed at two week intervals. This enabled us to follow NO_3^- production throughout the incubation. Potential nitrification was defined as the quantity of NO_3^--N in incubated samples in excess of initial amounts. Similarly, potential mineralization was calculated as the sum of extracted NH_4^+-N and NO_3^--N produced during incubation minus initial quantities.

Plate 4.1 Oblique view of the ground flora in Red Cedar Natural East Lansing, Michigan, U.S.A. Allium tricoccum and Asarum canadense dominate the ground flora in April when the photograph was taken. The scale in the foreground is 10 centimeters.

A modified *in vivo* assay based on NO_2^- formation was used to determine NR activity (Jaworski 1971; Klepper et al. 1971). Experiments were conducted to optimize enzyme activity and identify tissues most active in NO_3^- reduction. Enzyme activity was maximized by determining optimum combinations of NaH_2PO_4 (buffer), KNO_3 (substrate), $CH_3(CH_2)_2OH$, and pH. Five levels of each of these factors were used in a completely randomized design with replication. The optimal pH and proportions of NaH_2PO_4, KNO_3 and $CH_3(CH_2)_2OH$ were determined by analysis of variance for 4 x 5 factorial treatments in a completely randomized design with replication (SAS 1982). Treatment means were compared with Fisher's protected LSD (SAS 1982). T-tests for paired observations were used to test for differences in root and shoot NR activity.

Intact specimens of *Allium tricoccum* and *Asarum canadense* were collected from six random locations within the Red Cedar Natural Area. Plant samples were returned to the laboratory where they were washed with deionized water and refrigerated prior to analysis. Leaf tissue was cut into 4 mm x 10 mm strips and roots were cut into 10 mm lengths. Approximately 250 mg of tissue were placed in a chilled vial containing 5 ml of incubation medium. Two drops of chloramphenicol (0.5 mg/g) were added to preclude the development of prokaryotic NO_3^- reduction. Four replicate plant samples were incubated in the dark at 30° C for 1.5 h.

Nitrite production was measured initially and at 15 minute intervals by removing 0.4 ml aliquots of medium. Color development for NO_2^- determination was produced by adding 0.3 ml of 1% sulfanilamide-HCl and 0.3 ml of n-napthlyethylenediamine to each aliquot. After 20 minutes, samples were diluted with 20 ml of deionized water and absorbance was measured at 540 nm with a Beckman DU-24 spectrophotometer. A standard curve for NO_2^- was prepared before and after all analyses. NR activity was reported as activity per unit weight of fresh tissue.

Reduced pyridine nucleotide (NADH) is required for NO_3^- reduction within the plant cell cytoplasm (Bonner and Varner 1976; Beevers and Hageman 1980). Increased rates of respiration, resulting from elevated temperatures in the assay, may cause cytoplasmic NADH pools to vary and thus alter NO_3^- reduction. D-glucose can be used to increase cellular NADH pools and therefore increase NR activity if reducing power is limiting. Ten replicate assays were conducted with and without 2% D-glucose (weight per volume).

The presence of phenolic compounds, which may be liberated from disrupted plant tissue, may also limit NO_3^- reduction. Phenolic compounds are believed to combine reversibly with plant proteins through H-bonding and irreversibly by covalent interactions (Loomis and Battaile 1966). Bovine serum albumin (BSA) was added to interact with free phenolics and thereby reduce their effect on NR activity. Ten replicate assays were conducted with and without 10% BSA (weight per volume).

Estimates of NO_3^- reduction can also be affected by rates of biochemical NO_2^- removal from the assay via NO_2^- reduction. We checked for significant NO_2^- removal by following NO_2^- consumption from the incubation medium. Ten replicate assays were conducted with NO_2^- as substrate for shoot tissues of both herbaceous species. T-tests for paired observations were used to determine the effect of D-glucose, BSA and NO_2^- consumption on NR activity (Ecosoft 1984).

Direct Comparison of Plant NR Activity and Laboratory Nitrification Potential

Soil and plant samples were collected from six random locations in Baker Woodlot and Red Cedar Natural Area. At each sampling point, intact plants of *Allium tricoccum* and *Asarum canadense* were collected along with two soil samples 10 cm in depth. Individual plants were collected in close proximity to one another; soil samples taken directly beneath them were composited in the field. Laboratory mineralization and nitrification potential were determined by aerobic soil incubations as described above.

NR activity was measured for shoot tissue of each species by the above described procedure. To determine total N, a subsample of shoot tissue was oven dried at 70° C for 24 hours, after which it was ground and digested in concentrated H_2SO_4, with K_2SO_4 and HgO as catalysts. Total N was determined with a Technicon Autoanalyzer II (Technicon 1976). Soil variables and plant total N were tested as predictors of NR activity with a step-wise linear regression procedure (Ecosoft 1984).

NO_3^- Fertilization and NR Induction in *Asarum canadense* Clones

Clones of *Asarum canadense* were fertilized with KNO_3 to determine the extent of *de novo* NO_3^- reductase formation. Six individual clones were identified June 10, 1985 in Baker Woodlot and Red Cedar Natural Area. Within each clone, two 1-m^2 plots were established. Deionized water was applied to one plot (control) while the other was fertilized with 60 kg N/ha as KNO_3.

Fertilization treatments were made in two applications of 30 kg N/ha 78 hours apart. Leaf tissue was collected 78 hours after final application by randomly selecting 10 plants within each plot. Plant shoot tissue was composited by plot and analyzed for NR activity and total N by the above procedures. Treatment means were compared using t-tests for paired observations (Ecosoft 1984).

NO_3^- Fertilization and NR Induction in *Asarum canadense* Clones within Isolated Plots

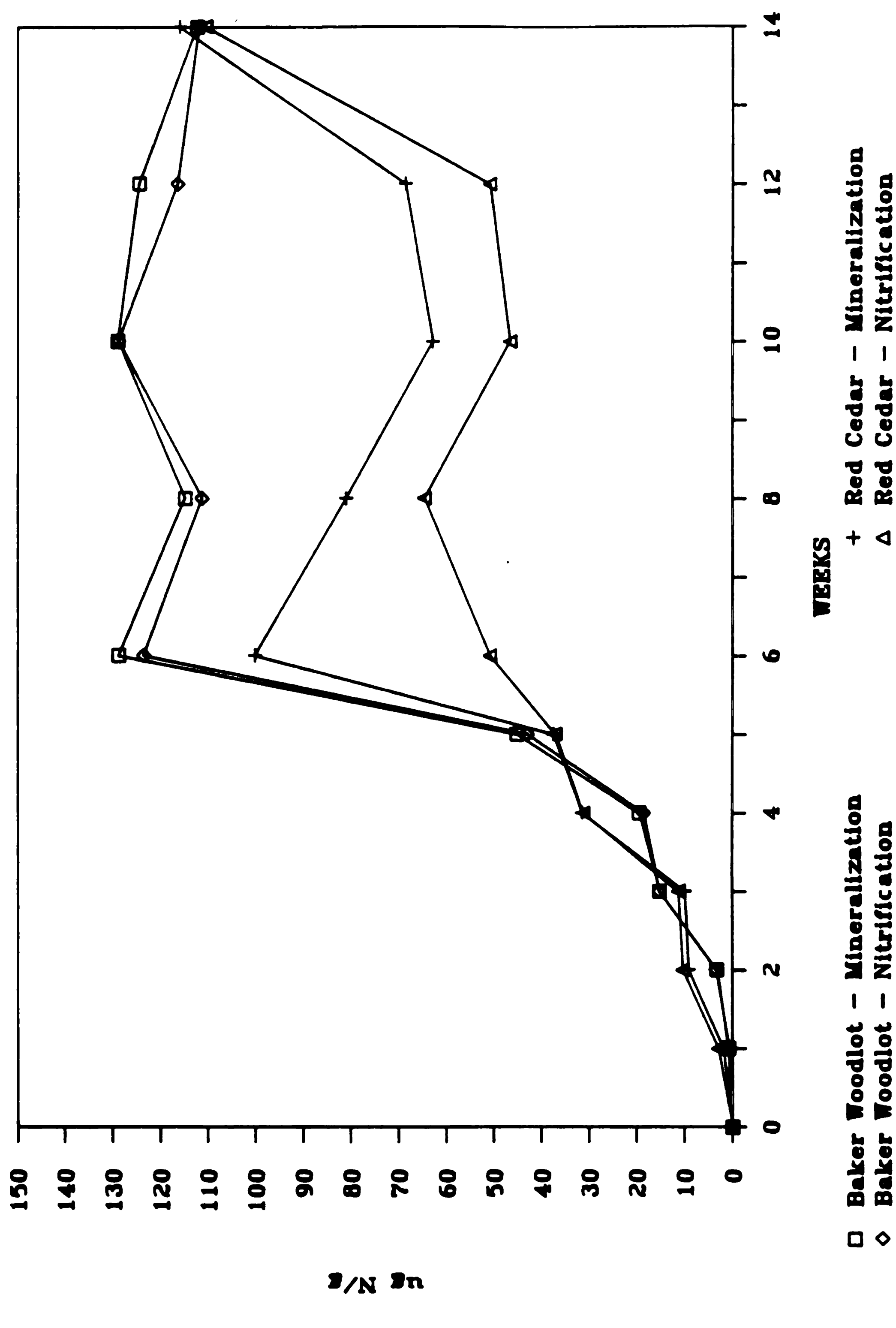
The perimeters of the 1-m^2 plots established in Experiment 2 were trenched to a depth of 40 cm to preclude N uptake by overstory and herbaceous plants outside of the plots. Trenching was conducted 5 and 10 days prior to the start of the experiment on August 12, 1985. Plots were again fertilized with 60 kg N/ha as NO_3^- in two equal additions separated by 78 hours. Equal volumes of deionized water were added to control plots. Shoot tissue was collected 78 hours after treatment for determination of NR activity and total N as described in the previous experiments. Treatment means were compared using t-tests for paired observations (Ecosoft 1984).

Results and Discussion

Nitrification Potential and NRA Optimization

Production of mineral N and NO_3^- in the soils followed a sigmoidal pattern over the 14 week incubation. Rates of potential mineralization and nitrification were highest between weeks 4 and 6 (Figure 4.1); NO_3^- was always the most abundant form of mineral N. Nitrification was active in both forest soils; 99% of the mineral N at the termination of the incubation was NO_3^-.

Figure 4.1 Potential N mineralization and nitrification in laboratory incubations for Baker Woodlot and Red Cedar Natural Area.


ug N/g
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WEEKS
□ Baker Woodlot - Mineralization
◇ Baker Woodlot - Nitrification
+ Red Cedar - Mineralization
Δ Red Cedar - Nitrification

Values reported for mineralization and nitrification agree with those reported for similar hardwood forests (Chapter II).

The components of the optimum NR activity assay for leaf and root tissues of *Allium tricoccum* and *Asarum cancdense* are listed in Table 4.1. The addition of D-glucose and bovine serum albumin did not significantly increase NR activity in any tissue, suggesting that neither reducing substrate or interference by phenolic compounds limited NR activity. Furthermore, NO_2^- consumption from the medium was insignificant when compared to its initial concentration.

Leaf tissue of both species had significantly greater NR activity than root tissue (Table 4.2). Nitrite, the product of NR, is further reduced to NH_3 in the chloroplast by a NADPH-linked NO_2^- reductase (Bonner and Varner 1976; Beevers and Hageman 1980). Some plants, however, have the ability to reduce substantial amounts of NO_3^- within root tissue (Townsed 1970; Stewart et al. 1972; Smith and Rice 1983). In terms of magnitude, reduction of NO_3^- in the roots of the species we studied was not important. However, the values reported for NO_3^- reduction in *Allium* roots may be underestimated since anaerobic assay conditions are known to enhance activities (J.A. Lee, personal communication).

NR activity was low in the leaves of both species when compared with other plants known to utilize NO_3^-, such as

Table 4.1 Components of the optimized incubation medium for leaf and root tissues of *Asarum canadense* and *Allium tricoccum*.

	Asarum canadense		*Allium tricoccum*	
	Leaf	Root	Leaf	Root
NaH_2PO_4	100 mM	100 mM	100 mM	100 mM
KNO_3	150 mM	100 mM	150 mM	150 mM
$CH_3(CH_2)_2OH$	1 %	3 %	3 %	3 %
pH	7.0	7.0	8.5	8.5

Table 4.2 Nitrate reductase activity for shoot and root tissue of *Asarum canadense* and *Allium tricoccum*. Values listed are mean activities (standard deviations). Plants were collected 27 April 1985 in Red Cedar Natural Area, E. Lansing, Michigan, U.S.A.

	Asarum canadense		*Allium tricoccum*	
	Leaf	Root	Leaf	Root
	nmoles NO_2^- g^{-1} hr^{-1}			
Plant				
1	165 (20.1)	20 (1.5)	30 (11.1)	7 (1.0)
2	225 (10.2)	13 (0.6)	11 (1.0)	10 (2.0)
3	191 (15.9)	6 (1.7)	30 (5.3)	8 (0.5)
4	208 (20.5)	17 (1.0)	24 (3.2)	6 (0.5)
5	111 (38.0)	10 (0.5)	24 (1.2)	5 (1.2)
6	75 (9.9)	9 (2.0)	23 (4.2)	7 (0.5)
Mean*	163a (5.7)	13b (5.0)	24x (9.0)	7y (4.0)

* Means were compared using a t-test for paired observations. Shoot and root activity were compared for each species. Means with the same letter are not significantly different at alpha = 0.001

cultivated and ruderal species (Table 4.3). Activities for *Asarum canadense* and *Allium tricoccum* leaf tissue were 163 and 24 nmoles NO_2^- g^{-1} hr^{-1}, respectively. These activities are 10 to 50 times lower than those reported for cultivated and ruderal plant species (Table 4.3). Activities greater than 1000 nmoles NO_2^- g^{-1} hr^{-1} have been considered significant in N nutrition (Havill et al. 1974), but the activities reported here are much lower (Table 4.2).

We found these low NR activities suprising in light of the high nitrification potentials of these sites. High nitrification potentials should relate to high NR activity if i) laboratory conditions accurately simulate field conditions or ii) NR activity accurately indexes the plants ability to assimilate NO_3^-. Alternatively, soil and plant samples were collected at different times; one year apart. Therefore, temporal variation may have contributed to these inconsistencies.

Direct Comparison of Plant NR Activity and Nitrification Potential

To accommodate differences in the preliminary study, plant NR activity and nitrification potential were measured simultaneously in Baker Woodlot and Red Cedar Natural Area. The proportion of pre-incubation NH_4^+ and NO_3^- were equivalent in soils of Baker Woodlot. Nitrate concentrations in Red Cedar Natural Area were two - times greater than NH_4^+.

Table 4.3 Nitrate reductase activity for selected groups of herbaceous and woody plants.

	Nitrate Reductase Activity nmoles NO_2^- g^{-1} hr^{-1}
I. Cultivated Species	
Glycine max cv. Dare	4280 (Jaworski 1971)
Cucurbita pepo	4280 (Routley 1972)
Lycopersicon esculentum	3700 (Routley 1972)
Nicotina tabacum	1280 (Routley 1972)
II. Ruderal Species	
Urtia dioica	7930 (Havil et. al 1974)
Galium aparine	4983 (Havil et. al 1974)
Rumex sanguineus	4360 (Havil et. al 1974)
Poa annua	4050 (Havil et. al 1974)
III. Ericaeous Species	
Kalmia lattifolia	142 (Routley 1972)
Vaccinium macrocarpon	50 (Routley 1972)
Ledum groenlandicum	0 (Smirnoff et al. 1984)
IV. Woody Species	
Pinus sylvestris	640 (Smirnoff et al. 1984)
Picea abies	250 (Smirnoff et al. 1984)
Thuja placata	20 (Smirnoff et al. 1984)
Tsuga heterophylla	10 (Smirnoff et al. 1984)

Following incubation, nitrogen mineralization and nitrification potentials were comparable to those measured at 6 weeks in the preliminary study (Figure 4.1 and Table 4.4). However, mineralization and nitrification potentials assayed in this second experiment were somewhat lower in Baker Woodlot, compared to levels in the preliminary study.

A linear regression model was used to predict nitrification potential using N mineralization potential as the independent variable. The relationship was highly significant ($p < 0.001$) with a coefficient of determination equal to 0.997 (r^2). The slope of the prediction equation (b_1) was 1.037. This indicates that a proportional relationship existed between N mineralization and nitrification in which virtually all the NH_4^+ produced was oxidized to NO_3^-.

Since initial root NR activities were low in both species (Table 4.3), NR activity was subsequently measured only in leaf tissues. Asarum canadense and Allium tricoccum leaf tissue exhibited low NR activity in both forest types (Table 4.4). Allium tricoccum leaf NR activity was equivalent in both forests, while, Asarum canadense had higher activities in the Red Cedar Natural Area than in Baker Woodlot (Table 4.4). Activities for Asarum canadense in Baker Woodlot and Red Cedar Natural Area were 28.8 and 40.0 nmoles NO_2^- g^{-1} hr^{-1}, respectively. Leaf total N was high for Asarum canadense and Allium tricoccum in both forests;

Table 4.4 Nitrate reductase activity of *Asarum canadense* and *Allium tricoccum* shoot tissue in relationship to soil N minerailzation and nitrification. Plants were collected in Baker Woodlot and Red Cedar Natural Area, E. Lansing, Michigan. Soil variables and shoot total N were used to predict nitrate reductase activity for each species. Values listed are means (standard deviation).

	Extractable NH_4^+-N	Extractable NO_3^--N	Potential* Mineralization	Potential* Nitrification	Shoot Total N	Shoot NO_3^- Reductase
	ug/g				— % —	nmoles NO_2^- g^{-1} hr^{-1}
I. Baker Woodlot						
Soil	2.3 (0.51)	2.5 (0.98)	67.8 (19.12)	67.8 (18.98)		
A. canadense					4.25 (0.73)	28.8 (4.32)
A. tricoccum					4.92 (0.49)	8.5 (1.39)
II. Red Cedar						
Soil	3.0 (0.64)	6.2 (1.77)	82.4 (24.75)	82.3 (24.09)		
A. canadense					4.85 (0.28)	40.0 (16.39)
A. tricoccum					4.04 (0.25)	8.5 (0.90)

* After 8 week laboratory incubations

values exceeded 4.0 % for both species (Table 4.4).

The step-wise regression model predicting NR activity from the variables in Table 4.4 was highly significant ($p < 0.01$; $r^2 = 0.67$). Extractable NO_3^- and nitrification potential were positively correlated with NR activity in Asarum canadense and were the only variables retained in the prediction model. In contrast, none of the plant and soil variables listed in Table 4.4 were correlated with NR activity in Allium tricoccum.

Nitrate reductase in many plants is associated with the quantity of NH_4^+ and NO_3^- within the soil. High levels of NO_3^- promote NR synthesis and activity, whereas NH_4^+ is inhibitory (Bonner and Varner 1976; Beevers and Hageman 1980). Results of the regression analyses suggest Asarum canadense has at least some ability to use NO_3^- for biosynthesis. It seems reasonable to expect such a correlation since enzyme synthesis and activity are induced by the presence of NO_3^-. The lack of correlation between soil and plant variables and Allium tricoccum NR activity suggests that this species was unable to assimilate NO_3^-. These results agree with other reports which have suggested that NH_4^+ may play a more critical role than NO_3^- in the nutrition of late successional plants (Bate and Heelas 1975; Franz and Haines 1977; Haines 1977; Smith and Rice 1983).

NO_3^- Fertilization and NR Induction in *Asarum canadense* Clones

Allium tricoccum completes most of its above ground growth early in the growing season and was senescent in June when the fertilization experiments were initiated. Therefore, we used individual clones of *Asarum canadense* which were persistent throughout the growing season. Nutrient additions resulted in a NO_3^-:NH_4^+ ratio in excess of 150 within the top 10 cm of soil in fertilized plots. In Baker Woodlot, fertilized plots had significantly greater NR activity and total N than the paired controls which received deionized water (Table 4.5). Similarly, fertilized plots in Red Cedar Natural Area had significantly greater NR activity compared to control plots (Table 4.5). However, there was no difference in total N between fertilized and control treatments in Red Cedar Natural Area (Table 4.5).

The increases in NR activity between control and fertilized plots were small and quantitatively insignificant. Smith and Rice (1983) found NO_3^- enrichment stimulated NO_3^- reduction in seral old field plants. Climax species, however, showed little response. Similar patterns have been demonstrated for other plant species and ecosystems (Dirr et al. 1974; Bate and Heelas 1975; Franz and Haines 1977). Induced enzyme activities in *Asarum canadense* were approximately 30 times less than endogenous activities of ruderal and cultivated plants (Table 4.3). Results of this

Table 4.5 Nitrate reductase activity and total N for *Asarum canadense* leaf tissue in Baker Woodlot and Red Cedar Natural Area. Plots were fertilized with 60 kg/ha of nitrogen added as NO_3^-. Values listed are means (standard deviation).

		Nitrate Reductase nmoles NO_2^- g^{-1} hr^{-1}		Total Nitrogen ug/g	
	CLONE	CONTROL	FERTILIZED	CONTROL	FERTILIZED
I. Baker Woodlot					
	1	16 (5.5)	26 (1.7)	3.13	3.12
	2	26 (1.7)	38 (4.1)	2.18	3.95
	3	16 (4.9)	24 (2.1)	2.43	4.25
	4	22 (3.6)	33 (1.9)	3.49	3.97
	5	23 (3.6)	66 (5.4)	3.29	3.70
	6	30 (0.8)	24 (2.8)	3.54	3.80
	MEAN	22.4*	35.4*	3.01*	3.80*
	S.D.	(5.9)	(15.1)	(0.52)	(0.34)
II. Red Cedar Natural Area					
	1	22 (3.3)	34 (4.3)	3.72	3.57
	2	23 (1.5)	23 (2.7)	3.57	3.78
	3	12 (1.3)	17 (2.7)	3.88	4.05
	4	24 (1.3)	25 (1.8)	3.76	3.89
	5	22 (1.5)	39 (2.6)	3.53	3.54
	6	31 (0.8)	36 (2.8)	3.61	3.71
	MEAN	22.4*	29.1*	3.61	3.84
	S.D.	(5.66)	(8.18)	(0.20)	(0.16)

* - Means were compared with a t-test for paired observations. Means were significantly different at alpha = 0.05

experiment also suggest that Asarum canadense has a limited ability to form NR. Therefore, NO_3^- should play a minor role in the N nutrition of this species. Alternatively, suppressed NR activity might be the result of root competition for NO_3^- from other members of the plant community leaving a small proportion of the added NO_3^- available for uptake by Asarum canadense. This alternative was addressed in the final experiment where the perimeter of each plot was trenched to preclude root competition from overstory and herbaceous plants.

NO_3^- Fertilization, and NR Induction in Asarum canadense Clones within Isolated Plots

Patterns of leaf NR activity and total N were identical to those in the first fertilization experiment. Within both forests, plants which received NO_3^- fertilization and trenching had significantly greater NR activity than controls (Table 4.6). However, induced rates of NO_3^- reduction were still much lower than rates cited as contributing significantly to plant N nutrition (Havill et al. 1974). In general, fertilized plants had higher leaf total N than the controls. In Baker Woodlot, leaf tissue total N was significantly greater in fertilized plants compared to controls. In contrast, no differences in total N were present in Red Cedar Natural Area (Table 4.6).

Table 4.6 Nitrate reducatse activity and total nitrogen for *Asarum canadense* in Baker Woodlot and Red Cedar Natural Area. Plots were fertilized with 60 kg/ha N applied as NO_3^- and the perimeter was trenched to preclude uptake by other plants. Values are means (standard deviation).

		Nitrate Reductase nmoles NO_2^- g^{-1} hr^{-1}		Total Nitrogen ug/g	
I. Baker Woodlot	CLONE	CONTROL	FERTILIZED	CONTROL	FERTILIZED
	1	15 (1.0)	24 (1.7)	3.25	3.13
	2	19 (2.3)	22 (3.3)	3.26	3.55
	3	11 (1.2)	17 (1.2)	3.35	3.41
	4	15 (0.8)	20 (0.5)	2.85	3.46
	5	19 (2.4)	34 (6.4)	3.11	3.91
	6	18 (0.8)	20 (1.2)	2.95	3.15
	MEAN S.D.	16.3* (3.2)	22.9* (6.2)	3.21* (0.2)	3.42* (0.3)
II. Red Cedar Natural Area					
	1	36 (1.3)	46 (2.2)	3.06	3.63
	2	39 (1.8)	36 (8.5)	3.73	3.66
	3	36 (3.6)	32 (0.8)	3.73	3.66
	4	33 (2.5)	40 (1.7)	3.46	3.64
	5	42 (2.1)	44 (5.4)	3.28	3.53
	6	37 (2.3)	52 (3.7)	3.15	3.55
	MEAN S.D.	36.4* (3.7)	41.1* (7.8)	3.41 (0.3)	3.61 (0.1)

* - Means were compared with a t-test for paired observations. Means are significantly different at alpha = 0.05.

Our results suggest that NO_3^- uptake by overstory and herbaceous plants did not limit NR induction in Asarum canadense; induced rates of enzyme activity were comparable in both fertilization experiments. Nitrate additions totaled 120 kg N/ha, a value comparable to the amount of N cycled annually in a northern hardwood forest (Whittaker et al. 1979). Certainly, NO_3^- additions of this magnitude should result in enzyme induction if this ability were inherent. The lack of biologically significant rates of NO_3^- reduction suggests that Asarum canadense has adapted to habitats low in available NO_3^-. Havill et al. (1974) have suggested that NR activity in excess of basal rates should represent a response proportional to nitrification. The herbs we studied appear to be adapted to NH_4^+ utilization.

The conflict between NR activity and nitrification potential may have resulted from an overestimation of actual soil nitrification. Alternatively, NR activity in these plants, however carefully optimized, may not be comparable to other species, since the assay was developed for early successional plants. The inherent limitation of N within temperate forests suggests strong competition for this resource among plants and between plants and microorganisms. Aside from a usable source of energy (carbon), microbial productivity is most limited by N (Stotzky 1972). Plant competition for N is eliminated in laboratory incubations and therefore NH_4^+ has two possible fates i) immobilization into microbial biomass and ii) oxidation to NO_3^- by nitrifying bacteria. Sieving of soil samples may temporarily reduce C limitations which would result in a stimulation of net mineralization producing a larger pool of NH_4^+ potentially available for nitrification.

Mineralization and nitrification potentials should more accurately represent in situ rates if samples were less disturbed (e.g. unsieved) and incubated for a shorter duration. Initial rates of mineralization and nitrification in the preliminary study were quite low and did not rapidly increase until 6 weeks. Perhaps short-term laboratory incubations are more indicative of the actual infield processes. The large increase in mineralization and nitrification potentials at week 6 are likely the result of microbial populations responding to reduced C and N limitations.

The limited ability of Asarum canadense and Allium tricoccum to assimilate NO_3^- suggests that nitrification may be a minor process in Baker Woodlot and Red Cedar Natural Area. However, these soils contained a viable inoculum of nitrifying bacteria able to respond when substrate was available for growth. Our results imply that competition for NH_4^+ among plants and nitrifying bacteria may be one mechanism of N retention by the vernal dam.

In the soil, most microorganisms remain attached to clay colloids (Bitton and Marshall 1980). Cell motility, which requires great expenditures of energy, is uncommon within the energy limited soil volume (Grey and Williams 1971). Therefore, soil microorganisms obtain nutrients for growth and maintenance through mass flow and sorption-accumulation effects at the surface of clay colloids (Filip et al. 1972). Nitrifying bacteria are not of the rhizosphere community and therefore reside within the bulk soil volume (Rovira 1965). In contrast, plant roots grow throughout the soil volume and have the ability to respond to localized nutrient concentrations. The capacity to exploit new soil volumes undoubtedly provides a competitive advantage to the plant over the immobile microorganism.

Our results provide indirect evidence for the importance of plant roots and their effect on N transformations. The removal of plant roots in the laboratory incubations undoubtedly provided increased levels of substrate for nitrification. It seems that N retention by the spring herb community occurs through NH_4^+ uptake, which circumvents nitrification and NO_3^- export. The extent of competition between plants and microorganism within the soil is not easily determined but may be approached through isotope dilution techniques. Further investigation is needed into the mechanism of N retention by spring herb communities, since our results only provide indirect evidence.

Conclusions

In the mesic late successional forests we studied, NO_3^- assimilation by the ground flora community seems minimal, suggesting that NH_4^+ uptake is perhaps the mechanism of N retention by the vernal dam. In contrast, nitrification potentials within these soils were high. The conflict between plant NR activity and nitrification potential may be attributable to i) overestimation of in situ nitrification under laboratory conditions, or ii) underestimation of NR activity in late successional species.

Plant root competition is eliminated in the laboratory incubations, thereby leaving more NH_4^+ for immobilization into microbial biomass and for nitrification. Nitrification may be rapid in soils where net mineralization is high and physical factors do not preclude nitrifier activity. This situation may arise in the laboratory where conditions for mineralization and nitrification are optimal. Alternatively, NR activity may be underestimated in late successional species, since the assay was developed for ruderals. Therefore, cross-species comparisons may not be valid.

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Chapter V

CONCLUSIONS

1. Landscape patterns of community composition and soil can be used to predict rates of intraecosystem N cycling. Forest ecosystems with different species composition and structure, growing on different soils will likely exhibit distinct patterns of N mineralization and nitrification.

2. The development of a conceptual model describing the spatial dynamics of N mineralization and nitrification requires the consideration of factors that influence both intraecosystem N cycling and ecosystem development. A parallel pattern between community composition and N turnover exists because i) the spatial distribution of forest communities is related to climate, physiography and soil (e.g. moisture availability), ii) the chemical composition of plant litter is related to species composition and plant nutrient use efficiency and iii) the activities of soil microorganisms, which make N available for plant uptake, are regulated in part by litter recalcitrance and soil moisture.

3. Nutrient cycling studies conducted within the framework of an ecosystem classification system can provide a

highly utilitarian way to extrapolate N cycling information across regional and local landscapes.

4. Nitrate loss following disturbance, such as forest management practices which eliminate plant uptake, seem probable within the sugar maple-basswood/Osmorhiza forests where extractable NO_3-N and nitrification were high throughout the year. Such losses seem of less consequence in the sugar maple-red oak/Maianthemum and black oak-white oak/Vaccinium ecosystems.

5. Nitrification was minimal within the black oak-white oak/Vaccinium ecosystem, even under laboratory conditions conducive to this process.

6. Plant species characteristic of diverse spring ephemeral and herbaceous ground flora communities were consistently related to high laboratory and in situ rates of nitrification.

7. The mechanism of N retention by spring ephemeral communities seems to be NH_4^+ assimilation which circumvents nitrification and the loss of NO_3^- to ground water and denitrification. However, further investigation is needed into the mechanism of the vernal dam, since these results only provide indirect evidence. The problem may be directly approached by using a stable isotope of N to trace the flow of N into plant biomass,

microbial biomass, available soil pools and into the atmosphere.

APPENDIX A

Location of Study Sites

LOCATION OF STUDY SITES

I. sugar maple-basswood/Osmorhiza Stands

A. Stand 6

Legal Description - NE 1/4, NW 1/4, Sec.17, T 21 N, R 11 W

The stand is adjcent to State Route M-55; take a small two-track 1.3 miles from S 13 Rd (Cabrefae Rd.). Proceed 3 chains north on the two track to a triple stumped beech marked with an X. The main plot is 3 chains at 314°. The directions to each plot are given in distance and azmuth from main plot. Locations of plots in the remaining stands are described in this manner.

	Azmuth	Chains
Plot 1 -	234°	2.5
Plot 2 -	187°	5.0
Plot 3 -	299°	1.6
Plot 4 -	224°	1.6

B. Stand 22

Legal Description - SE 1/4,SW 1/4, Sec. 24, T 23 N, R 12 W

From State Route M-115 in Mesick, turn South on the road that runs between the Mesick High School and the Stadium (N 13 Rd.). Take this road until it dead ends into a T intersection. Head east (left turn) approxamately 0.3 miles and turn south (right turn) onto a small dirt road. Proceed approximately 0.3 miles until reaching a run-down tar paper shack on the west side of the road. At the south most corner of the lot lies a small Forest Service access road; take this road 0.5 miles into the hills. The road climbs a steep hill and the stand lies over the crest where the road levels. Main pit - 220°; 1.5 chains

	Azmuth	Chains
Plot 1 -	322°	1.7
Plot 2 -	174°	1.5
Plot 3 -	234°	1.5
Plot 4 -	Main Plot	

C. Stand 24
Legal Description - SE 1/4,SW 1/4, Sec. 10, T 21 N, R 12 W

The stand lies directly north of State Route M-55, Turn north off of M-55 onto Forest Service Rd. 5339, there is a white wagon wheel attached to the sign post at the intersection of this road and M-55. Proceed 25 ft. north onto Forest Service Rd. 533 before coming to a small two track on the east side of the road. The two track parallels M-55 and passes through a small white spruce planting. Proceed 0.2 miles to the stake on the north side of the road. The stand is north of the two track. The stand is bordered by a small draw on its east boundary; two plots lie along its west side. Main plot 232°; 6.0 chains from X of double stump sprout black cherry.

	Azmuth	Chains
Plot 1 -	186°	3.1
Plot 2 -	311°	2.4
Plot 3 -	25°	2.6
Plot 4 -	Main Plot	

II. sugar maple-red oak/Maianthemum stands

A. Stand 7
Legal Description - N 1/2, NW 1/4, Sec. 29, T 21 N, R 11 W

The stand lies on the south side of Hoxyville Rd. and its boundaries are defined by 2 two tracks that encircle the stand. The stand is located, if coming from the east, aon the first crest of a large hill. From Hoxyville Rd., the stand is entered by climbing a steep hill and traveling directly south; the main pit lies 9.5 chains at 274 ° from the X on a tree.

	Azmuth	Chains
Plot 2 -	187°	5.0
Plot 4 -	224°	1.6
Plot 5 -	135°	3.1
Plot 6 -	Main Plot	

B. Stand 41
Legal Description - NE 1/4, SE 1/4, Sec. 35, T 23 N, R 10 W

Take Forest Service Rd. 5348 north 0.6 miles from the three way intersection at the NW corner of Sec 2 and the

NE corner of Sec 1. The Stand lies on the west side of the road where it takes a sharp bend to the right. Turn west on to a two track and proceed 2.3 chains to an X on a double stump sprout red maple. Continue 9.0 chains at 270° to the main plot.

	Azmuth	Chains
Plot 1 -	86°	3.4
Plot 2 -	232°	2.7
Plot 3 -	326°	1.9
Plot 4 -	Main Plot	

C. Stand 56
Legal Description - SE 1/4, NW 1/4, Sec. 25, T 22 N, R 12 W

The stand is at the southern crest of a large hill on the road between Cabrefae Ski Area and Harrieta. It is 4.0 miles N of M-55 on S 13 Rd. and 1.8 miles N of the ski area. Directly behind the stand is a large TV tower. A sugar maple is marked with an X between the first and second sand dune. From the tree, proceed 4.9 chains at 314° to the main plot.

	Azmuth	Chains
Plot 1 -	246°	2.9
Plot 2 -	48°	1.7
Plot 3 -	140°	2.6
Plot 4 -	Main Plot	

III. black oak-white oak/Vaccinium stands

A. Stand 3
Legal Description - NE 1/4, SW 1/4, Sec. 31, T 22 N, R 15 W

From State Route M-55, take Skokelgas Rd. heading north from the Star Corners 3 miles. Take Becker Rd. heading west, it will run due west for 1.5 miles before it makes a few bends as it passes a large farm. The stand lies approximately 0.3 miles from the last corner where the road heads southwest. The stand lies at the top of a plateau on the southeast side of the road. A 24 inch red oak is marked with an X; from here proceed 6.1 chains at 124° to the main plot.

	Azmuth	Chains
Plot 1 -	4°	1.5
Plot 2 -	238°	2.5
Plot 3 -	73°	1.5
Plot 6 -	Main Plot	

B. Stand 9
Legal Description - SE 1/4, NW 1/4, Sec. 11,
T 22 N, R 14 W

The stand is 1 mile north of Brethern, 2.2 miles on Brewer Rd. The stake is adjcent to a 26" dbh black oak in the north side of the road. The main plot is 75 ft at 348°.

	Azmuth	Chains
Plot 1 -	100°	4.2
Plot 2 -	79°	4.9
Plot 3 -	188°	2.7
Plot 4 -	Main Plot	

C. Stand 58
Legal Description - NE 1/4, NW 1/4, Sec. 16,
T 22 N, R 13 W

The stand is 0.6 miles north of Red Bridge Rd. on Forest Service road 5022. A small two track runs northwest from 5022; take it 50 ft to a small turnout. An X is marked on a 14" black oak. Main plot is 5.0 chains at 316°.

	Azmuth	Chains
Plot 1 -	260°	3.0
Plot 2 -	64°	2.5
Plot 3 -	336°	2.8
Plot 4 -	Main Plot	

APPENDIX B

Table B.1 Summary of selected herbaceous and woody ground flora species from three upland forests. Values represent average coverage (%) determined by ocular estimation.

ECOSYSTEM	black oak-white oak/ Vaccinium															
STAND	3	3	3	3	9	9	9	9	52	52	52	52	58	58	58	58
PLOT	1	2	3	6	1	2	3	4	1	2	3	4	1	2	3	4
Vaccinium angustifolium	4.5	9.33	4	1.08	3	10.5	3.33	6.25	0	8.91	0.66	13.4	2.5	1	21.5	30
Gaultheria procumbens	0.166	0.16	0.41	0.08	1.41	0.41	2.25	0.83	0	0	0	0	0.42	0.75	3.08	1.41
Melanpyrum lineare	0.75	0	0	0.01	0	0	0	0.09	0	0.01	0	0	0.01	0	0	0.41
Gaylussacia baccata	0	0	8.33	0	0	0	0	0	0	0.84	0.09	3.33	0	0	0	0
Leucobryum glaucum	0	0.08	0.01	0.66	0	0	0	0	0	0	0	0	0	0	0	0
Trientalis borealis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0.84
Carex pensylvanica	2.416	1.08	4.08	1.42	13.5	2.75	2.50	3	0.08	0.16	0.08	0	5.58	5.83	0.36	0.75
Hamamelis virginiana	8.333	0.41	0.33	0.33	0	0	0.08	0	0.33	0	0.41	0	0	0	0	0
Smilacina racemosa	0	0	0	0	0.08	0	0	0	0.01	0	0	0	0	0	0	0
Dicranum polysetum	0	0.33	0	0	0.33	0	0.08	0.41	0	0	0	0	0.34	0.33	0	0
Pteridium aquilinium	6.25	12.0	4.58	0.33	2	8.16	1.75	0.33	3.08	0.41	0.33	0.33	0.34	4.16	10	4.91
Orysopsis asperifolia	0	0.01	0.1	0	0	0	0	0	0	0	0	0.08	0	0.01	0	0
Viburnum acerifolium	0	0	0	0	0.08	0	0	0	0.42	0	0	0	0.33	0.33	0.33	0
Carex sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopodium obscurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maianthemum canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aralia nudicaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monotropa uniflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus ideaus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allium tricoccum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmorhiza chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Botrychium virginianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trillium grandiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex plantaginea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonatum biflorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago caesaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes cynosbati	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium robertianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium trifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium boreale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiarella cordifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mitella diphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hepatica acutiloba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uvularia perfoliata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dirca palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caulophyllum thalictroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table B.1 Continued

ECOSYSTEM	sugar maple-red oak/ *Maianthemum*															
STAND	7	7	7	7	25	25	25	25	41	41	41	41	56	56	56	56
PLOT	2	4	5	6	1	2	3	4	1	2	3	4	1	2	3	4
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaultheria procumbens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melanpyrum lineare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaylussacia baccata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucobryum glaucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trientalis borealis	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pensylvanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hamamelis virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilacina racemosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum polysetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteridium aquilinium	19.1	20.8	1	4.16	0	0	0	0	0	0	0	0	0	0	0	0
Orysopsis asperifolia	0	0	0.66	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum acerifolium	0	0	0	0	0	0	0	0	0	0	0	0	1.66	0	0	0
Carex sp.	0	0	0	0	0.33	0	0	0	0.33	0.16	0	0	0.67	0	0	0
Lycopodium obscurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Maianthemum canadense	0.66	0.5	0.08	0	0	0	0	0	0	0.08	0	0	0.58	0.16	0.58	0.42
Aralia nudicaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0
Monotropa uniflora	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus ideaus	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allium tricoccum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmorhiza chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Botrychium virginianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trillium grandiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex plantaginea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonatum biflorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago caesaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes cynosbati	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium robertianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium trifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium boreale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiarella cordifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mitella diphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hepatica acutiloba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uvularia perfoliata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dirca palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caulophyllum thalictroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table B.1 Continued

ECOSYSTEM	sugar maple-basswood/ Osmorhiza															
STAND	2	2	2	2	6	6	6	6	22	22	22	22	24	24	24	24
PLOT	1	3	4	6	1	2	3	4	1	2	3	4	1	2	3	4
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaultheria procumbens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melanpyrum lineare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaylussacia baccata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucobryum glaucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trientalis borealis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pensylvanica	1.41	5.91	0	0	0.33	0	0	0	0	0	0	0	0.42	0.01	0	r
Hamamelis virginiana	0	0	0	0	0.08	0	0	0	0	0	0	0.01	0	2	0	0
Smilacina racemosa	0	0	0	0	0.25	0.41	0	0	0	0.66	0	0.33	0	0	0	0
Dicranum polysetum	0.08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteridium aquilinium	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orysopsis asperifolia	0.75	4	0.16	0.33	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum acerifolium	0	1.66	0.33	0	0	0	0	0	0	0	0.08	0	2.33	0	0.33	0
Carex sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopodium obscurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maianthemum canadense	0	0.51	0.75	1.41	0.41	3.75	0.5	0	0.08	0	0.34	0	0.01	0.01	0	0
Aralia nudicaulis	0	0.08	0	0.33	23.3	1.66	0	29.5	0	0	0.75	0	0	0	1.83	1.75
Monotropa uniflora	0	0	0	0	0.01	0	0.01	0	0	0	0	0	0	0	0	0
Rubus ideaus	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0.66	0.41	0.01	2.5	2.5	3	8.5	0.34	0.03	0	0.01	2.33	0.75	2.41	0.09
Allium tricoccum	0	0	0	0	6.5	0.16	3.08	1	0.58	1.41	0.35	1.75	2.41	30.8	35	16.4
Osmorhiza chilensis	0	0	0	0	17.5	11.1	17.8	15	0.76	4.34	5.41	2.5	1.09	7.33	5.33	4.66
Botrychium virginianum	0	0	0.08	0.08	1.83	0.08	2	0.33	0	0.33	0.33	0.33	0	0.08	0	0
Trillium grandiflora	0	0	0.34	0.08	6.16	0.41	0.41	0.33	0	0	0.08	0	0	0.08	0.16	0.33
Carex plantaginea	0	0.33	0.66	0	0.75	0	0	1.66	0	0	0.33	0.33	1.66	0.41	0.33	1
Polygonatum biflorum	0.66	0.01	0	0.42	0.33	0	0	0	0	0.33	0.41	1.08	0	0	0.01	0
Solidago caesaria	0	0	0.08	0.41	0	0	0	0	0.42	0.41	0.67	0.33	0.08	0	0	0
Ribes cynosbati	0	0	0	0	0.75	1.66	0.33	2	0	0	0	0.33	0.66	0	0.33	0
Geranium robertianum	0	0	0	0	0	0	0	0	0.18	0.75	0.43	0.75	0.01	0	0	0
Galium trifolium	0	0	0	0	0.41	0	0	0.33	0	0	0	0	0.33	0.41	0.33	0
Galium boreale	0.41	0.08	0	0	0.41	0	0.41	0	0	0	0	0	0.33	0	0	0
Tiarella cordifolia	0	0	0	0	0	0	0	0	0.08	0	0	0	1.66	6.16	0.34	2
Mitella diphylla	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0.66	0	0.01
Hepatica acutiloba	0	0.33	0	0	0	0	0	0	2.00	0	0	0	0	0.33	0	0.34
Uvularia perfoliata	0.33	1	0	0.83	0	0	0	0	0	0	0	1.66	0	0	0	0
Dirca palustris	13.4	1.66	1.66	4.83	0	0	0	0	0	0	0	0	0	0	0	0
Caulophyllum thalictroides	0	0	0	0	0	0	0	0	0	2	0	0	0	0.33	0	8.33